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UNIVERSITY OF ALBERTA

SOME EFFECTS OF DEFOLIATION ON PLAINS ROUGH FESCUE (*Festuca hallii* (Vasey) Piper) IN CENTRAL ALBERTA

BY

PERCY RUSSELL HORTON

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

IN

RANGE SCIENCE

DEPARTMENT OF PLANT SCIENCE

EDMONTON, ALBERTA

SPRING 1991

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ISBN 0-315-66770-2

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DEGREE: DOCTOR OF PHILOSOPHY

YEAR THIS DEGREE GRANTED: 1991

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Andrew

ABSTRACT

Festuca hallii (Vasey) Piper is the dominant species in the *Festuca-Stipa* grasslands of the Aspen Parkland ecoregion of Alberta. It is a key species which has been recognized for its grazing value, but it has decreased on, or been eliminated from, many *Festuca-Stipa* grasslands because of poor range management practices. The Aspen Parkland ecoregion supports at least 30% of the provincial beef herd; therefore information is needed for better management of *Festuca hallii*.

Research was conducted on an undisturbed *Festuca-Stipa* grassland site. The growth pattern and forage quality of *Festuca hallii* was monitored during 1987. Season of defoliation treatments (annual cuts in May, June, July, August, September, and October) and frequency of defoliation treatments (1, 2, 4, and 8-cuts annually) were applied from 1985 to 1987. Parameters evaluated included aboveground dry matter yield (DMY), sward composition, phenology, leaf height and senescence, forage nutritional characteristics, inflorescence density, tiller density; stem base: weight, total nonstructural carbohydrate percentage (TNC (%)), TNC pool; and root weight to a 7.5 cm depth of *Festuca hallii*. The vigor of *Festuca hallii* after twelve years of grazing under light June, heavy June, heavy continuous, heavy autumn and light autumn grazing regimes at a second site was evaluated by etiolated regrowth measurements.

The growing season study indicated rapid growth and phenological change with decreased TNC (%) in stem bases from early May to early June for *Festuca hallii*. Crude protein yield in foliage peaked in September and was associated with a low lignin content. Early June was the most sensitive period while early July and early October were the least sensitive periods for season of defoliation stress. Four or eight defoliations per growing season resulted in reductions in aboveground DMY, sward composition, tiller density, end-of-season stem base: weight, TNC pool, and root weight. All grazing regimes resulted in vigor loss for *Festuca hallii* with minimum loss in autumn grazed pastures. There were vigor increases for other species for all grazing regimes, except the light autumn regime.

These results suggest that *Festuca hallii* is suited to summer and autumn grazing or a deferred rotation grazing system.

ACKNOWLEDGEMENTS

To Gail, whose vision, encouragement, employment, and sacrifices made this venture possible. Perhaps, only the spouses of other Ph.D. students, who have worked and parented alone in the stressful and uncertain vacuum that these programmes can generate know the depth of the contribution made.

To Dr. Art Bailey (Plant Science), who sponsored and initially supervised an African sojourner's long time interest in graduate level range science training. For friendship, advice, and encouragement spanning nearly a decade, thank you. To Dr. Jane King (Plant Science), for her consistent friendship, encouragement, constructive critique, and willingness to step in as co-supervisor during Dr. Bailey's sabbatical. To Dr. John Hoddinott (Botany), for his steady involvement on the supervisory committee and superb teaching of plant physiology.

To other faculty members who have each contributed important and strategic components to my graduate schooling process: Dr. Keith Briggs (Plant Science), Dr. David Chanasyk (Soil Science), Dr. Edwin Cossins (Botany), Dr. Mark Dale (Botany), Dr. Dhara Gill (Rural Economy), Dr. Bob Hardin (Animal Science), Dr. Bob Hudson (Animal Science), Dr. George La Roi (Botany), Dr. Byron Kratochvil (Chemistry), Dr. Gary Mathison (Animal Science), Dr. Walter Moser (Botany), Dr. Steve Pawluk (Soil Science), Dr. Mick Price (Animal Science), Dr. Bill Vanden Born (Plant Science), and Dr. Peter Walton

(Plant Science). A special thank you to Dr. Chanasyk for his interest and assistance from the initial block burning to the development of the soil water and soil temperature study which was conducted concurrently with the results reported in this thesis.

To Mrs. Verna Clarke, who so ably kept the administrative details of my programme in order, thank you. To Mr. Barry Irving and Mr. Mike Willoughby who provided able technical assistance, advice and comradeship. To Mr. Gerry Hoppe, Dr. Anne Naeth, and Mr. Mike Willoughby who, as fellow graduate students, provided a forum for the exchange of many ideas and techniques. A very very special thank you to Gerry who so willingly shared his experience in both the lab and the field and worked unstintingly through the summers of 1986 and 1987. To the summer students who assisted each year at the University of Alberta ranch, thank you.

To the statisticians of the Computing Services Department with a special thank you to Dr. Terry Taerum who patiently assisted with this project from beginning to end. A special thank you to Mr. Ray Weingardt of Animal Science for his statistical coaching.

To Dr. Nancy Cyr and Dr. Mac Efloson (retired) of the Alberta Research Council for their nuclear magnetic resonance work on the forage quality of *Festuca hallii*. To Dr. Bob Howitt of the Alberta Research Council and Mr. David Lloyd of Alberta Forestry, Lands and Wildlife for their field inspections and classification of the soil pits at the research site.

To the Agriculture Canada Research Branch and in particular, the directors of the Melfort Research Station, Dr. Stan Beacom (1966-1989) and Dr. Harmon Davidson (1989-present), who facilitated the completion of this Ph.D project while I was simultaneously employed as the station's forage agronomist. To the members of the station's forage agronomy group, Mr. Maurice Hiltz, Mrs. Brenda Sorensen, Mr. Harry Tkachuk and Mr. Laurie Vhal for their 'training' of a new scientist while he was otherwise occupied.

Finally my deep appreciation to my parents, Dr. Don and Margaret Horton, whose practical assistance and effective grandparenting enabled the completion of the final draft.

To each of the above, and to anyone who I may have missed, my sincere appreciation for your contributions to this project.

TABLE OF CONTENTS

I. INTRODUCTION....1

The Fescue Grasslands Of Western Canada....1

Why *Festuca hallii* ? - Taxonomy and Nomenclature....3

The Importance of the Fescue Grasslands in Alberta....7

Defoliation Effects....8

Rangeland Community Dynamics....8

Grass Plant Dynamics....12

Factors Influencing Defoliation Effects....16

Season....17

Frequency....17

Intensity....18

Duration....18

Hypothesis To Be Tested....18

Literature Cited....19

II. EXPERIMENTAL LOCATION, GEOLOGY, SOILS, CLIMATE, VEGETATION AND DESIGN.....25

Experimental Location.....25

Study Sites and Experimental Design.....25

Geology.....29

Soils.....32

Climate.....39

Vegetation.....47

Literature Cited.....49

III. GROWTH AND FORAGE QUALITY OF PLAINS ROUGH FESCUE IN A *FESTUCA-STIPA* GRASSLAND IN CENTRAL ALBERTA.....53

Introduction.....53

Materials and Methods.....55

Study Area and Experimental Design.....55

Dry Matter Yield and Sward Composition.....57

Leaf Height and Senescence.....58

Growth Stage.....58

Forage Quality of *Festuca hallii*..........58
Stem Base Weight, TNC (%), TNC Pool and Root Weight....59
Statistical Analysis..........61
Results..........61
Dry Matter Yield..........61
Sward Composition..........68
Leaf Height and Senescence..........70
Growth Stage..........74
Forage Quality..........74
Stem Base Weight, TNC(%), and TNC Pool..........81
Root Weights..........83
Discussion..........83
Sward Dynamics..........83
Festuca hallii Dynamics..........86
Conclusions..........94
Literature Cited..........96

IV. EFFECTS OF SEASON OF DEFOLIATION ON PLAINS ROUGH FESCUE IN CENTRAL ALBERTA....101

Introduction....101

Materials and Methods....104

Study Area and Experimental Design....104

Sward Dry Matter Yield....106

Sward Composition....107

Inflorescence Density....109

Tiller Density....110

End-of-season Stem Base Weight, TNC (%), and TNC Pool, and Root Weight....110

Statistical Analysis....112

Results....113

Sward Dry Matter Yield....113

Sward Composition....122

Inflorescence Density....129

Tiller Density....131

End-of-season Stem Base Weight, TNC (%), and TNC Pool....136

Root Weight..139

Discussion..143

Sward Responses - Yield and Species Composition.........143

Festuca hallii Responses - Morphological and
Physiological..151

Conclusions..162

Literature Cited..164

V. SOME EFFECTS OF FREQUENCY OF DEFOLIATION ON PLAINS ROUGH
FESCUE IN CENTRAL ALBERTA..170

Introduction..170

Materials and Methods..174

Study Area and Experimental Design..174

Sward Dry Matter Yield..176

Sward Composition..177

Inflorescence Density..179

Tiller Density..179

End-of-season Stem Base Weight, TNC(%), TNC Pool,
and Root Weight..180

Statistical Analysis....181

Results....182

Sward Dry Matter Yield....182

Sward Composition....195

Inflorescence Density....202

Tiller Density....206

End-of-season Stem Base Weight, TNC (%), and TNC Pool....209

Root Weight....218

Discussion....221

Sward Responses - Yield and Sward Composition....221

Festuca hallii Responses - Morphological and Physiological....225

Defoliation Treatment Effects....235

Conclusions....238

Literature Cited....239

VI. VIGOR OF PLAINS ROUGH FESCUE UNDER VARIOUS SEASONS AND INTENSITIES OF GRAZING IN CENTRAL ALBERTA.....246

Introduction.....246

Materials and Methods.....249

    Study Area and Experimental Design.....249

    Etiolated Regrowth.....253

    Statistical Analysis.....254

Results.....255

    Etiolated Regrowth.....255

Discussion.....262

    Etiolated Regrowth of Nongrazed Plants.....262

    Etiolated Regrowth of Grazed Plants.....264

    Etiolated Regrowth of Grazed versus Nongrazed Plants.....265

    Species Composition of Etiolated Regrowth in 1985.....270

Conclusions.....271

Literature Cited.....272

VII. RESEARCH SYNTHESIS....................277
Growth and Forage Quality Factors of *Festuca hallii*....................277
Sward Responses....................280
Festuca hallii Responses....................283
Defoliation Treatment Effects....................286
Management Implications....................288
Literature Cited....................290

LIST OF TABLES

Table 1.1 Comparison of *Festuca altaica*, *Festuca campestris*, *Festuca hallii* characteristics 5

Table 2.1 Long-term grazing regimes imposed on a *Festuca-Stipa* grassland in central Alberta 28

Table 2.2 Monthly precipitation, monthly precipitation as a percentage of the long-term (1962-1980) average, and 1987 precipitation as a percentage of the 1986 precipitation at the University of Alberta ranch headquarters, Kinsella, Alberta....44

Table 2.3 Accumulated monthly precipitation, accumulated monthly precipitation as a percentage of the long-term (1962-1980) average, and 1987 accumulated precipitation as a percentage of 1986 accumulated precipitation at the University of Alberta ranch headquarters, Kinsella, Alberta 45

Table 2.4 Average monthly temperature and monthly difference from the long-term (1962-1980) monthly average temperature at the University of Alberta ranch headquarters, Kinsella, Alberta....................46

Table 3.1 Coefficients of determination for sward dry matter yield (SWYL), *Festuca hallii* (*Fh*) dry matter yield (FHYL), other grasses and grass-like plants dry matter yield (OGYL), forbs and woody dry matter yield (FWYL), *Fh* sward composition (FHSW%), other grasses and grass-like plants (OGSW%), forbs and woody species (FWSW%), *Fh* extended leaf height (ELH), *Fh* green leaf height (GLH), *Fh* crude protein (CP%), *Fh* crude protein yield (CPYL), *Fh* neutral detergent fibre (NDF%), *Fh* acid detergent fibre (ADF%), *Fh* hemicellulose (HC%), *Fh* cellulose (CL%), *Fh* acid detergent lignin (ADL%), *Fh* stem base weight (SBWT), *Fh* stem base total nonstructural carbohydrate percentage (SBTNC%), *Fh* stem base total nonstructural carbohydrate pool (SBTNCPL) and *Fh* root weight (RTWT) as a function of Julian date in 1987 using linear, quadratic, cubic, quartic and quintic regressions..........64

Table 3.2 Growth stage; foliage: crude protein percentage (CP), crude protein yield (CPYL), neutral detergent fibre percentage (NDF), acid detergent fibre percentage (ADF), acid detergent lignin percentage (ADL), cellulose percentage (CL), hemicellulose percentage (HC); and stem base total nonstructural carbohydrates percentage (TNC) for *Festuca hallii* by sampling date in 1987..........75

Table 4.1 Date of May, June, July, August, September, and October season of defoliation treatments and date of collection of sward composition, inflorescence density, tiller density, and stem base core samples for 1985, 1986, and 1987..........108

Table 4.2 Mean square values of aboveground dry matter yield for the total sward, *Festuca hallii*, other grasses and grass-like species, forbs, and woody species in the May, June, July, August, September, and October defoliation treatments for 1986 and 1987....114

Table 4.3 Aboveground dry matter yield of the total sward in the May, June, July, August, September and October defoliation treatments for 1986 and 1987....116

Table 4.4 Aboveground dry matter yield of *Festuca hallii*, other grasses and grass-like species, forbs, and woody species in the May, June, July, August, September, and October defoliation treatments for 1986 and 1987....119

Table 4.5 Mean square values of sward composition for *Festuca hallii*, other grasses and grass-like species, forbs, and woody species in the control, burnt control, May, June, July, August, September, and October defoliation treatments for 1986 and 1987....123

Table 4.6 Sward composition of *Festuca hallii*, other grasses and grass-like species, forbs, and woody species in the control, burnt control, May, June, July, August, September, and October defoliation treatments for 1986 and 1987....125

Table 4.7 Mean square values of the inflorescence density of *Festuca hallii* in the control, burnt control, July, August, September, and October defoliation treatments for 1986 and 1987....130

Table 4.8 Inflorescence density of *Festuca hallii* in the control, burnt control, July, August, September, and October defoliation treatments for 1986 and 1987........132

Table 4.9 Mean square values of tiller density, stem base dry matter (DM) weight, stem base total nonstructural carbohydrate (TNC) percentage, stem base TNC pool, and root DM weight to a 7.5 cm depth for *Festuca hallii* in the control, burnt control, May, June, July, August, September, and October defoliation treatments for 1986 and 1987........134

Table 4.10 Tiller density of *Festuca hallii* in the control, burnt control, May, June, July, August, September, and October defoliation treatments for the combined 1986 and 1987 data........137

Table 4.11 End-of-season (October) stem base dry matter weight, stem base total nonstructural carbohydrate (TNC) percentage, and stem base TNC pool for *Festuca hallii* in the control, burnt control, May, June, July, August, September, and October defoliation treatments for 1986 and 1987........140

Table 4.12 End-of-season (October) root dry matter weights to a 7.5 cm depth for *Festuca hallii* in the control, burnt control, May, June, July, August, September and October defoliation treatments in 1986 and 1987........141

Table 5.1 Dates of the 1, 2, 4, and 8-cut frequency of defoliation treatments and date of collection of sward composition, inflorescence density, tiller density, and stem base core samples for 1985, 1986, and 1987 178

Table 5.2 Mean square values of aboveground dry matter yield for the total sward, *Festuca hallii,* other grasses and grasslike species, forbs, and woody species in the 1, 2, 4, and 8-cut defoliation treatments for 1986 and 1987 183

Table 5.3 Aboveground dry matter yield (DMY) of total sward, *Festuca hallii,* grasses and grass-like species, forbs, and woody species in the 1, 2, 4, and 8-cut defoliation treatments, with percentage change of DMY in the 2, 4, and 8-cut defoliation treatments over that in the 1-cut treatment, for 1986 and 1987 185

Table 5.4 Dry matter yield of *Festuca hallii* foliage regrowth by defoliation cut number and treatment total in the 1, 2, 4, and 8-cut defoliation treatments for 1986 and 1987 190

Table 5.5 Mean square values of sward composition for *Festuca hallii*, other grasses and grass-like species, forbs, and woody species in the 1, 2, 4, and 8-cut defoliation treatments for 1986 and 1987 196

Table 5.6 Sward composition of *Festuca hallii*, other grasses and grass-like species, forbs, and woody species in the control, burnt control, 1, 2, 4, and 8-cut defoliation treatments, with percentage change of sward composition in the control, burnt control, 2, 4, and 8-cut defoliation treatments over that in the 1-cut treatment, for 1986 and 1987 197

Table 5.7 Mean square values of the inflorescence density of *Festuca hallii* in the control, burnt control, 1-cut, and 2-cut defoliation treatments for 1986 and 1987 203

Table 5.8 Inflorescence density of *Festuca hallii* in the control, burnt control, 1, 2, 4, and 8-cut defoliation treatments, with percentage change of the control, burnt control, 2, 4, and 8-cut defoliation treatments over the 1-cut treatment, for 1986 and 1987 204

Table 5.9 Mean square values of tiller density, stem base dry matter (DM) weight, stem base total nonstructural carbohydrate (TNC) percentage, stem base TNC pool, and root DM weight to a 7.5 cm depth in the control, burnt control, 1, 2, 4, and 8-cut defoliation treatments for 1986 and 1987 207

Table 5.10 Tiller density of *Festuca hallii* in the control, burnt control, 1, 2, 4, and 8-cut defoliation treatments, with percentage change of tiller density in the control, burnt control, 2, 4, and 8-cut defoliation treatments over that in the 1-cut defoliation treatment, for the combined 1986 and 1987 data 208

Table 5.11 End-of-season (October) stem base dry matter weight, stem base nonstructural carbohydrate (TNC) percentage, and stem base TNC pool of *Festuca hallii* in the control, burnt control, 1, 2, 4, and 8-cut defoliation treatments, with percentage change of stem base dry matter weight, stem base TNC percentage, stem base TNC pool in the control, burnt control, 2, 4, and 8-cut defoliation treatments over that in the 1-cut treatment for 1986 and 1987......212

Table 6.1 Long-term grazing regimes imposed on a *Festuca-Stipa* grassland in central Alberta......252

Table 6.2 Mean square values of etiolated regrowth dry matter yield for nongrazed and grazed *Festuca hallii*, and nongrazed and grazed other species, in the Light June, Heavy June, Heavy Continuous, Heavy Autumn, and Light Autumn grazing regimes for 1984 and 1985......256

Table 6.3 Etiolated regrowth of *Festuca hallii* in the nongrazed (NG) and grazed (G) treatments of the Light June, Heavy June, Heavy Continuous, Heavy Autumn, and Light Autumn grazing regimes, with the percentage change of the etiolated regrowth in the grazed over nongrazed treatments of each grazing regime for 1984, 1985, and 1984 and 1985 combined......257

Table 6.4 Etiolated regrowth of the other species in the nongrazed (NG) and grazed (G) treatments of the Light June, Heavy June, Heavy Continuous, Heavy Autumn, and Light Autumn grazing regimes, with the percentage change of the etiolated regrowth in the grazed over nongrazed treatments of each grazing regime for 1984, 1985, and 1984 and 1985 combined......258

LIST OF FIGURES

Figure 2.1 Aerial view of Section 28 26

Figure 2.2 Schema of randomized block design for season of defoliation and frequency of defoliation experiments 30

Figure 2.3 A common soil-plant community association on southern exposures in Section 28 33

Figure 2.4 Climate diagram for long term (1962-1980) temperature and precipitation at Kinsella, Alberta 42

Figure 2.5 Long term (1962-1980) precipitation and potential evapotranspiration (ET) for Kinsella, Alberta 43

Figure 3.1 Sward aboveground dry matter (DM) yield of *Festuca hallii*, other grasses and grass-like species, and forbs and woody species through the 1987 growing season by sampling date 62

Figure 3.2 Dry matter (DM) yield of a *Festuca-Stipa* sward through the 1987 growing season as a function of Julian date 65

Figure 3.3 Dry matter (DM) yield of *Festuca hallii* through the 1987 growing season as a function of Julian date 66

Figure 3.4 Dry matter (DM) yield of the other grasses and grass-like species through the 1987 growing season as a function of Julian date........67

Figure 3.5 Dry matter (DM) yield of the forbs and woody species through the 1987 growing season as a function of Julian date........69

Figure 3.6 Sward composition of *Festuca hallii*, other grasses and grass-like species, and forbs and woody species through the 1987 growing season by sampling date........71

Figure 3.7 Extended leaf height (ELH) and green leaf height (GLH) of *Festuca hallii* through the 1987 growing season as a function of Julian date........73

Figure 3.8 Crude protein percentage (CP (%)) and crude protein yield (CPYL) of *Festuca hallii* through the 1987 growing season as a function of Julian date........76

Figure 3.9 Neutral detergent fibre percentage (NDF (%)), acid detergent fibre percentage (ADF (%)), and cellulose percentage (CL (%)) of *Festuca hallii* through the 1987 growing season as a function of Julian date 78

Figure 3.10 Hemicellulose percentage (HC (%)) and acid detergent lignin percentage (ADL (%)) of *Festuca hallii* through the 1987 growing season as a function of Julian date........79

Figure 3.11 Stem base total nonstructural carbohydrate percentage (TNC (%)) of *Festuca hallii* through the 1987 growing season.....82

Figure 4.1 Aboveground dry matter (DM) yield of the sward by season of defoliation treatment for 1986 and 1987.....117

Figure 4.2 Aboveground dry matter (DM) yield of *Festuca hallii* by defoliation treatment for 1986 and 1987.....120

Figure 4.3 Sward composition of *Festuca hallii* by defoliation treatment for 1986 and 1987.....126

Figure 4.4 Inflorescence density (# m^{-2}) of *Festuca hallii* by defoliation treatment for 1986 and 1987.....133

Figure 4.5 Tiller density (# m^{-2}) of *Festuca hallii* by defoliation treatment for 1986 and 1987.....135

Figure 4.6 Root dry matter (DM) weight to a 7.5 cm depth for *Festuca hallii* by defoliation treatment in 1986 and 1987.....142

Figure 5.1 Aboveground dry matter (DM) yield of the sward by frequency of defoliation treatment for 1986 and 1987.....186

Figure 5.2 Aboveground dry matter (DM) yield of *Festuca hallii* by defoliation treatment for 1986 and 1987.....188

Figure 5.3 Accumulated dry matter (DM) yield of *Festuca hallii* foliage regrowth by cut number for the 4-cut defoliation treatment for 1986 and 1987.....191

Figure 5.4 Accumulated dry matter (DM) yield of *Festuca hallii* foliage regrowth by cut number for the 8-cut defoliation treatment for 1986 and 1987..192

Figure 5.5 Sward composition of *Festuca hallii* by defoliation treatment for 1986 and 1987..198

Figure 5.6 Inflorescence density of *Festuca hallii* by defoliation treatment for 1986 and 1987..205

Figure 5.7 Tiller density of *Festuca hallii* by defoliation treatment for 1986 and 1987..210

Figure 5.8 End-of-season stem base dry matter (DM) weight of *Festuca hallii* by defoliation treatment for 1986 and 1987...213

Figure 5.9 End-of-season stem base total nonstructural carbohydrate percentage (TNC (%)) of *Festuca hallii* by defoliation treatment for 1986 and 1987..215

Figure 5.10 End-of-season stem base total nonstructural carbohydrate (TNC) pool of *Festuca hallii* by defoliation treatment in 1986 and 1987..217

Figure 5.11 End-of-season root dry matter (DM) weight to a 7.5 cm depth of *Festuca hallii* by defoliation treatment for 1986 and 1987..220

Figure 6.1 Percentage change (% Δ) for *Festuca hallii* and the other species for nongrazed to grazed etiolated regrowth for the

Light June (L. June), Heavy June (H. June), Heavy Continuous (H. Con.), Heavy Autumn (H. Aut.) and Light Autumn (L. Aut.) grazing regimes....260

Figure 6.2 Etiolated regrowth of *Festuca hallii*, other grasses and grass-likes, and forbs and woody species for the Light June (L. June), Heavy June (H. June), Heavy Continuous (H. Con.), Heavy Autumn (H. Aut.) and Light Autumn (L. Aut.) grazing regimes for 1985....261

I. INTRODUCTION

A strategic objective in grazing management is establishment of the optimum defoliation regime for maximizing long term productivity of the key species of a given grassland. *Festuca hallii* (Vasey) Piper [1], or Plains rough fescue, is the key species of the native *Festuca-Stipa* grasslands of east-central Alberta. The specific purposes of this research project included the establishment of how the defoliation factors of season, frequency, and intensity affected certain biological and production parameters of *Festuca hallii*. The overall purpose of this research was to establish the response of *Festuca hallii* to differing frequencies, seasons and intensities of defoliation in order to make grazing management recommendations for optimizing its productivity within the *Festuca-Stipa* grasslands of east-central Alberta.

THE FESCUE GRASSLANDS OF WESTERN CANADA

Seven grassland associations have been identified in North America which extend from the edge of the coniferous forest in western Canada southward through the United States to the woodlands of central Mexico (Coupland 1979). To the east of the

---

[1] Scientific nomenclature follows Moss (1983) except where a different authority is cited in the text.

Rocky Mountains are the Fescue Prairie, Mixed Prairie, True Prairie, Desert Plains Grassland and Coastal Prairie grassland associations. To the west of the Rocky Mountains are the Palouse Prairie and Pacific Prairie grassland associations. In Canada, the two predominant grassland associations are the Fescue Prairie and the Mixed Prairie.

The Fescue Prairie or fescue grasslands in Western Canada have been described by several workers (Moss and Campbell 1947, Coupland and Brayshaw 1953, Coupland 1961, Blood 1966, Looman 1969, Looman 1981, Looman 1982). An overview of the fescue grasslands of western Canada from British Columbia to Manitoba was contributed by Looman (1969). Previously, the *Festuca scabrella* association in Alberta was described by Moss and Campbell (1947), in Saskatchewan by Coupland and Brayshaw (1953), and in Manitoba's Riding Mountain National Park by Blood (1966). For the three prairie provinces the fescue grasslands are primarily associated with the northern dark-gray and black soil zones which are more mesic than the dark brown and brown soil zones to the south. The dark gray soil zone and the northern edge of the black soil zones are also associated with the aspen parkland which is between the boreal forest to the north and the grasslands to the south (Bird and Bird 1967). The aspen parkland is characterized by a mosaic of fescue grasslands broken by groves of aspen (*Populus tremuloides*) and woodlands.

A more recent reconsideration of the fescue grasslands by Looman (1981, 1982) using Braun-Blanquet methodology has resulted in the following classification. His results placed the fescue grasslands of the prairie provinces in the Stipo-Festucetea class. The Stipo-Festucetea class was divided into two orders: the Danthonio-Festucetalia or mesic grasslands where the fescues were dominant under what were presumed to be natural conditions and the Stipetalia curtisetae or dry-mesic grasslands where the needle grasses were dominant. Looman then further divided the Danthonio-Festucetalia order into the Agropyrion spicatae alliance of southern Alberta, adjacent British Columbia and the northern United States, the Festucion hallii alliance of the prairie plains and the Festucion altaicae alliance of the subboreal zones of Alberta, British Columbia and Alaska. This work was important to recent revisions in the nomenclature for the rough fescues.

Why *Festuca hallii* ? - Taxonomy and Nomenclature

Historically the principal native grass in the *Festuca-Stipa* grasslands of the aspen parkland of central Alberta and the *Festuca-Danthonia* grasslands of the Rocky Mountain foothills of south-western Alberta has been called *Festuca scabrella*.

There has been considerable confusion in both the taxonomy and nomenclature of the rough fescues. The number of taxa assigned to the rough fescue complex has ranged from one (Johnston 1958, Moss 1983), to two (Piper 1906, Alexeev 1982), or even three (Pavlick and Looman 1984, Harms 1985, Looman and

Best 1987). Where more than one taxon has been used, the rank assigned has ranged from subvariety (Saint-Yves 1925), to variety (Gleason 1952, Breitung 1957a, 1957b), to subspecies (Harms 1985), to species (Rydberg 1922; Taylor and MacBryde 1977; Pavlick and Looman 1984; Looman and Best 1987).

The 1983 edition of Moss's *Flora of Alberta* (Moss 1983) does not distinguish the *Festuca scabrella* of the aspen parklands of central Alberta from that of the Rocky Mountain foothills of south-western Alberta. The two most recent taxonomic publications agree on three taxa but differ over ranking the taxa as species (Pavlick and Looman 1984) or subspecies (Harms 1985). Pavlick and Looman (1984) present a detailed morphological, chromosome number, and habitat separation of the three fescue taxa and their species ranking, namely, *Festuca altaica* Trin. *in* Ledeb., *Festuca campestris* Rydb., and *Festuca hallii* (Vasey) Piper (Table 1.1).

Festuca hallii plants are relatively short and grow in clumps 7-10 cm in diameter with up to 10 culms that are typically erect or slanting to 70 ° from the horizontal and they generally have creeping rhizomes. *Festuca campestris* plants are comparatively tall and form larger clumps, 25 to 30 cm in diameter, with up to 25 culms that typically slant 45 to 50 ° from the horizontal and they generally do not have creeping rhizomes. *Festuca altaica* plants are of intermediate height and form clumps with 5 to 10 culms that

Table 1.1 Comparison of *Festuca altaica*, *Festuca campestris*, *Festuca hallii* characteristics (adapted from Pavlick and Looman 1984).

Characteristic	*F. altaica*	*F. campestris*	*F. hallii*
Chromosome #	2n=28	2n=56	2n=28
Culm height, cm	30-70	40-90	28-51
Panicle length, cm	8-16	9-18	7-12
Panicle width, cm	5-13	2-6	2-3
Panicle attitude	nodding (erect?)	erect (nodding?)	erect
Spikelet length, mm	8-13	8-13	7-9
Spikelet floret #	3-4	3-5	2
Creeping Rhizomes	Infrequent	Infrequent	Frequent
Vegetation zones	Alpine, subalpine, boreal	Montane, subalpine	Plains, boreal, lower subalpine

have typically nodding panicles and they generally do not have creeping rhizomes.

Pavlick and Looman (1984) presented a geographic distribution for *Festuca hallii*, *Festuca campestris* and *Festuca altaica* in Canada and the northern United States which is consistent with the geographic separation of the taxa proposed by Harms (1985) and with the earlier work of Johnston and Cosby (1965). The geographic range of *Festuca hallii* runs in a northwesterly arc from North Dakota through Manitoba, central Saskatchewan and central Alberta, and then down a corridor to the east of the Rocky Mountain range from central Alberta through Montana, Wyoming and central Colorado (Pavlick and Looman 1984, Harms 1985). The lectotype of *Festuca hallii* (Vasey) Piper is from high elevations in Colorado (Pavlick and Looman 1984)

The species nomenclature for the North American rough fescues as proposed by Pavlick and Looman (1984) will be followed in this thesis. When literature cited refers to *Festuca scabrella*, an effort will be made to interpret that literature as *Festuca campestris* or *Festuca hallii* on the basis of the geographic distribution of taxa as presented by Pavlick and Looman (1984) and Harms (1985). *Festuca hallii* and *Festuca campestris* are commonly called plains rough fescue and foothills rough fescue, respectively.

THE IMPORTANCE OF THE FESCUE GRASSLANDS IN ALBERTA

The Aspen Parkland ecoregion of central Alberta and the Fescue Grass ecoregion of south-western Alberta together support at least 40% of the provincial beef herd on 13% of the province's total land area (adapted from Alberta Agriculture Statistics Branch 1984, Strong and Leggat 1981). In 1984, the Aspen Parkland ecoregion of central Alberta carried at least 1.0 million head or 30% of the province's total beef herd. In 1987, 30% of Alberta's farm cash receipts or $1,218,000,000 came directly from the sale of cattle and calves (Alberta Agriculture Statistics Branch 1989). While a precise estimate is not currently available, if it is assumed that one third of the forage input for the beef and calf sales from the Aspen Parkland ecoregion came directly from *Festuca-Stipa* grasslands, then the 1988 production value of these central Alberta native grasslands would have been in the order of $110,000,000.

Despite the intensive use of this native species, management for its optimal production is not widely practised due in part to: (1) the pervasive practice of continuous grazing in the prairie provinces (Walton et al. 1981), (2) lack of knowledge regarding the growth cycle of *Festuca hallii* and its consequent mismanagement and (3) lack of knowledge regarding which grazing regimes would enable the optimal utilization of *Festuca hallii*. The sensitivity of *Festuca hallii* to defoliation has been noted since the early survey work (Moss and Campbell 1947).

Bailey et al. (1980) have established that the production of the native *Festuca-Stipa* rangeland at the University of Alberta Ranch at Kinsella was equal to or better than the production of the cultivated *Bromus inermis-Festuca rubra* swards in the absence of a legume. Bailey et al. (1988) have also shown, in an 11-year grazing study on *Festuca-Stipa* rangeland at Kinsella, average daily gains for steers of 1.1 kg under light (8 animal unit months (AUM)) June grazing and 0.8 kg under light (8 AUM) autumn grazing. Most of this weight gain performance is attributable to *Festuca hallii* which may contribute more than 70% of the sward's dry matter production.

Therefore the determination of basic information on the response of this species to season, frequency and intensity of defoliation is both of scientific and economic importance for the establishment of optimum grazing management practices in central Alberta.

DEFOLIATION EFFECTS

Defoliation has a variety of effects on both the rangeland community as a whole and on the individual plants which make up a particular rangeland community.

Rangeland Community Dynamics

Defoliation has variable and complicated effects on a rangeland community as whole. This complicated response to defoliation is due to the variable responses of the individual member species of that community to a particular defoliation event. These responses are a function of the interaction between the individual plant's physiology and the season, frequency, intensity and duration of a particular defoliation application under given environmental parameters. Given this complicated response, certain important concepts for monitoring how defoliation affects a rangeland community as a whole have been developed. These concepts are termed key species, range condition and range trend.

Key species refer to those which must, because of their abundance and palatability, be considered in the management of a given rangeland community (Society for Range Management 1989). The key species are used to indicate degree of use, range condition and range trend for a given rangeland.

Range condition may be defined as: "The present state of vegetation of a range site in relation to the climax (natural potential) plant community for that site." (Society for Range Management 1989). Range trend refers to the direction of change in ecological status of a site, that is, whether a given rangeland community has a change in range condition through time that is toward, away from, or one which is not apparent, relative to the climax community for that site (Society for Range Management 1989).

The present use of the range condition concept is limited to native rangeland communities and is not applicable to grasslands which have a predominant component of introduced exotic species. Dyksterhuis (1949) proposed four range condition classes: excellent, good, fair, and poor, which were determined on the percentage of the climax vegetation in the sward composition for a given range site relative to its climax vegetation. The sward composition assessment is based on what was understood to be the species historically indigenous to a given site. These species are divided into two response categories: decreasers and increasers; based on how the sward composition (dry matter (DM%)) for a species changed with increasing grazing pressure. In general, the decreasers were the predominant and most palatable and nutritious species at a given site under low grazing pressure, but were most sensitive to increased grazing pressure. The increaser species became more prominent with increasing grazing pressure to a certain point, after which they too would decline with further increase in grazing pressure. The increasers were characterized by a greater degree of grazing resistance than the decreasers. This was often associated with a lower degree of palatability or nutrition. With further increases in grazing pressure, a third category of plants which Dyksterhuis (1949) called invaders became increasingly prominent. These species were not part of the climax community and invade a site as the decreasers and increasers both begin to disappear because of high levels of grazing pressure, thus generating further stages of retrogression.

The range condition and trend concepts based on the classification of species as decreasers, increasers and invaders as originally proposed by Dyksterhuis (1949) are a useful construct for evaluating how defoliation may be influence a given rangeland community. These constructs have a major weakness, however, where quality exotic species have been introduced to a deteriorated range site and are subsequently providing high yielding quality forage. The excellent range condition class is keyed to the premise of a native climax community which has reached its state by being protected from unnatural disturbances. This premise, therefore, creates a designation which provides no basis for incorporating the widespread introduction of productive exotic species which have over time become part of, or which may even come to dominate, a native range community.

Therefore the use of the concept of potential natural community versus that of climax community may be a better means of setting range condition classes. Potential natural community describes the biotic community that would become established on an ecological site if all the successional sequences were completed without interference by man, but allowing for natural disturbances and the introduction of naturalized non-native species (Society for Range Management 1989). An alternate and more radical refinement of the North American model of range condition might be the redefinition of the range condition classes along a continuum of overrested, optimum condition and overgrazed (Tainton 1981). This South African approach assumes a certain level of grazing pressure as a prerequisite for optimum range condition.

While there are limitations as discussed above, of the range condition concept based on Dyksterhuis's (1949) proposal, it still remains a useful guide for discussing the impact of defoliation on a rangeland community. It also remains a current operational tool for evaluating range condition and stocking rates on western Canadian rangelands (Wroe et al. 1988). It is useful in facilitating the determination of the key species upon which the management of a given rangeland should be based. Dyksterhuis's concepts will be utilized in this thesis for evaluating defoliation effects on the *Festuca-Stipa* grasslands of central Alberta.

Grass Plant Dynamics

Defoliation during the growing season alters the physiology and morphology of a grass plant. The degree of physiological and morphological change is a function of the season, frequency, intensity and duration characteristics of defoliation. Grass plant survival, dry matter yield, inflorescence production, tiller dynamics and root weights, following a defoliation event, are all related to both the nature of the defoliation event and a number of physiological and morphological characteristics peculiar to the specific grass plant at the time of defoliation. An understanding of the interaction between the defoliation characteristics of season, frequency, intensity and duration and the physiological and morphological characteristics of the key species through the growing season is strategic for the development of an optimum grazing management regime for a given rangeland.

Dry matter yield

Defoliation affects the grass plant by removing leaf and stem area, thereby reducing photosynthetic capacity. Repeated defoliations within the same growing season may, therefore, result in a loss of dry matter yield due to a reduction in the photosynthetic capacity of the plant. Therefore, the determination of how season, frequency, intensity and duration of defoliation affect a key species is important in terms of dry matter yield and carbon allocation. Caldwell et al. (1981) demonstrated striking physiological differences in carbon allocation to growing tissue following defoliation by comparing two *Agropyron* species of similar growth form and phenological characteristics. *Agropyron desertorum* was characterized by initiating new tiller formation and growth and the curtailment of root growth, following defoliation, preventing the depletion of the limited soluble carbon buffer. *Agropyron spicatum*, in contrast, was characterized by only limited new tiller development and continuous root growth, following defoliation, making the plant vulnerable to the depletion of its soluble carbon buffer. The differences in the response to defoliation between these two similar plants growing in the same environment illustrate how species-specific physiological mechanisms may influence dry matter yield, tiller density and grazing resistance following defoliation.

Inflorescence production

The timing of the initial defoliation within a growing season is a critical component in either suppressing or facilitating inflorescence production. Defoliation may also influence floral induction by habitat modification. This, in turn, may cause microclimatic changes which will facilitate or suppress floral induction and or initiation. Once floral initiation has taken place, season of defoliation may influence inflorescence production through the mechanical removal of developing or mature inflorescences.

Tiller dynamics

The tillering response of a grass plant to defoliation appears to be species-specific (Caldwell et al. 1981). Defoliation resistance would appear to be associated with the ability to allocate soluble carbon resources to the development of new tiller growth, with the simultaneous restriction of root growth following defoliation. Tiller density, regardless of the plant's tillering response to defoliation, may therefore provide an important indicator of defoliation stress. For those species which do not have tillering following defoliation, the loss of tiller density may be an important clue indicating their vulnerability to defoliation stress. For those species which have tillering following defoliation, loss of tiller density with increasing defoliation stress may be indicative of very serious defoliation stress.

Stem base weight, total nonstructural carbohydrate concentration (TNC (%)) and TNC pool

Total nonstructural carbohydrate concentration (TNC(%)) has been shown to vary through the year following a pattern associated with the phenological development of a number of range and forage grass species (Trlica 1977). Attention to defoliation management with respect to TNC (%) has been regarded as very important by a number of researchers for a long period of time. Certain types of TNC (%) patterns have been demonstrated to be associated with specific species and associated with greater or lesser degrees of defoliation tolerance (Menke and Trlica 1981). It has been commonly held that defoliation management which allowed for the recharge of the TNC (%) was vital to the longevity of a given species in a range community, especially as it related to the end of season levels and the ability of a species both to survive through a long cold winter and to initiate new foliage growth the following spring. More recent work has further clarified the role of TNC (%) following defoliation (Richards and Caldwell 1985). The role of stored TNC (%) in regrowth may be less important than previously thought for some species. For many species, concurrent photosynthesis following defoliation may have a more important contribution to regrowth than was previously recognized. The relative importance of soluble carbohydrates in regrowth following defoliation appears to be species-specific.

Where soluble carbohydrates are vital for regrowth following defoliation, the TNC pool (g m^{-2}) may be of greater importance than TNC (%). TNC pool is the product of the TNC (%) times the dry matter weight of the storage organ(s) measured.

Root dynamics

Increasing defoliation intensity has been shown to not only stop root growth, but progressively delay its restart, in certain grass species (Crider 1955). The response of root growth to defoliation has been shown to be species specific (Caldwell et al. 1981). Richards (1984) showed that the defoliation sensitive *Agropyron spicatum* appears to inflexibly allocate carbon below ground after severe defoliation, causing an imbalance of the root:shoot biomass proportions. In contrast, *Agropyron desertorum*, which is comparatively tolerant to defoliation, demonstrated a reduction of root growth following defoliation allowing for a more rapid reestablishment of the photosynthetic canopy and a balance between root and shoot. Therefore, the ability of a grass plant to reduce root growth following defoliation, in favor of reestablishment of the photosynthetic canopy area, may be an important factor in its ability to tolerate defoliation stress.

FACTORS INFLUENCING DEFOLIATION EFFECTS

How a defoliation event affects a rangeland and its constituent plants is dependent upon a number of factors which characterize that defoliation event. These factors are the season, frequency, intensity and duration of the defoliation event. Methods of defoliation include grazing, burning, mowing and clipping. The precise characteristics of the defoliation action may vary with type of animal used for grazing, the character of the fire used in a burn, and the style of mower or shears used in mowing and clipping. These biological and mechanical differences in the technique of defoliation do not automatically indicate different defoliation effects on the plants. In the *Festuca-Stipa* grassland of central Alberta, Sinton and Bailey (1980) demonstrated that defoliation by mowing and fire had almost identical effects on *Festuca hallii* as a function of season of defoliation.

Season

Season of defoliation refers to the time period in the growing season during which the defoliation event occurs. Investigations of effects of season of defoliation enable the determination of how defoliation at different points in the growth cycle of a plant or sward affect it.

Frequency

Defoliation frequency refers to how many times in a specified time period defoliation is repeated. Generally this time period is limited to the growing season of the plant or sward being investigated.

Intensity

Intensity refers to the height at which the defoliation occurs and, by implication, depending on the growth habit of the plant being evaluated, what proportion of the top growth of the plant is removed by that defoliation event. Defoliation by mowing results in a uniform height of defoliation. Defoliation by grazing results in a greater variation in the height of defoliation. Under grazing, the uniformity of height of defoliation will be a function of stocking rate and duration of defoliation.

Duration

Duration refers to the time period over which the defoliation event is applied. In the case of defoliation by mowing it is almost instantaneous, in the case of defoliation by fire it may range between seconds and minutes, and in the case of livestock grazing it may range from minutes to days depending on the stocking density and other management factors. In the research reported in this study, the mowing studies involved instantaneous and uniform defoliation. In the case of the grazing study, the defoliation treatments were applied through a time period of one month.

HYPOTHESES TO BE TESTED

The hypotheses tested in the mowing study were that season of defoliation and frequency of defoliation at a standardized intensity and duration have no effect on: 1) the dry matter yield and sward composition of a *Festuca-Stipa* grassland sward, and that 2) the dry matter yield, inflorescence production, tiller density, end-of-season stem base weight, total nonstructural carbohydrate concentration (TNC%), and TNC pool, and root weight to a 7.5 cm depth of *Festuca hallii* were also unaffected.

Using a long term grazing study, the hypotheses tested was that season and intensity of defoliation at a standardized frequency and duration had no effect on the etiolated regrowth of *Festuca hallii* and other associated species in a *Festuca-Stipa* grassland in east-central Alberta.

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II. EXPERIMENTAL LOCATION, GEOLOGY, SOILS, CLIMATE, VEGETATION AND DESIGN

EXPERIMENTAL LOCATION

The research reported in this thesis was conducted in the Aspen Parkland ecoregion as found in the eastern part of the County of Beaver in east-central Alberta in western Canada. The study area (53°N latitude and 112°W longitude) was located on the University of Alberta's research ranch 10 km north of the town of Kinsella, Alberta. Kinsella is approximately 150 km southeast of Edmonton, Alberta. The research was limited to Section 28, Township 47, Range 11, west of the 4th meridian. Elevation is approximately 700 m above sea level. Section 28 is a mosaic of natural aspen forest, shrub and grassland communities. Carrier Lake (55.8 ha) runs in a north-south direction though section 28 dividing it into a large west portion (180.9 ha) and a small east portion (22.5 ha).

Study Sites and Experimental Design

Two specific study sites were used in this research. One site was located on the west side and the other on the east side of Carrier Lake (Figure 2.1). The west site was utilized to investigate the specific effects of a long-term season and intensity of grazing

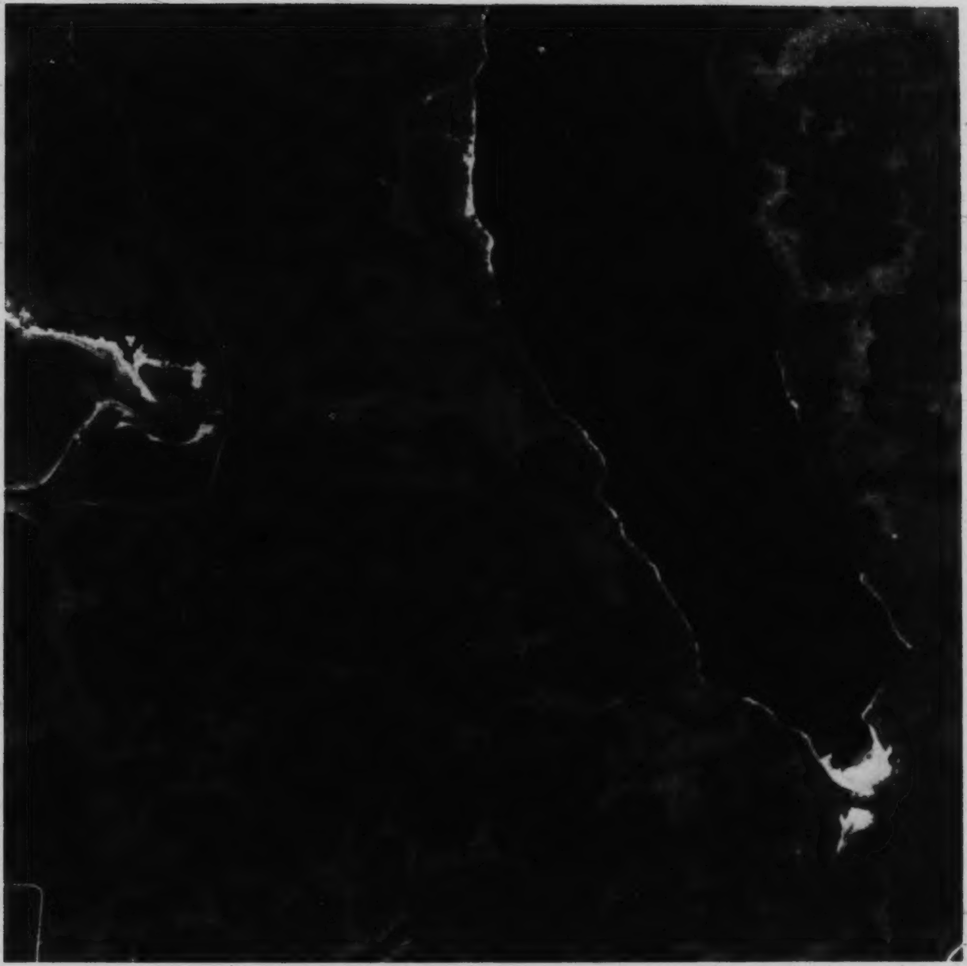

Figure 2.1 Aerial view of Section 28. The west study site was in the northwest quarter and the east study site was east of Carrier Lake. North is up on the page.

study on the vigor of *Festuca hallii* (Vasey) Piper[1]. This long-term grazing study was operated by Dr. A. W. Bailey from 1973 to 1988. The east site was used to investigate season and frequency of defoliation effects on the *Festuca-Stipa* sward in general, and *Festuca hallii* in particular.

The west study site was a long-term grazing experiment by Bailey et al. (1980, 1988) consisting of five long-term grazing treatments (Table 2.1). The purpose of this long-term grazing study was to compare the effects of season of grazing (June vs Autumn) and intensity of grazing (Light vs Heavy) with the widely practiced standard of Heavy Continuous Grazing on a *Festuca-Stipa* grassland. Each grazing regime was fenced to include 5.5 ha of grassland and a variable area of aspen forest and shrubland (Figure 2.1).

The east study site was a 22.5 ha wedge of the aspen parkland mosaic consisting of grassland (3.4 ha or 21%) and aspen forest and shrubs (17.8 ha or 79%) (Figure 2.1). This site had not been grazed for about 25 years (Bailey 1976). At the beginning of May, 1985, ten blocks within the grassland area were burnt to remove the heavy accumulation of litter. Control plots (2 X 10 m) were established adjacent to each burnt block. Within each burnt block two experiments were set up using a randomized design, with plots

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[1] Scientific nomenclature follows Moss (1983) except where a different authority is cited in the text.

Table 2.1. Long-term grazing regimes imposed on a *Festuca-Stipa* grassland in central Alberta (adapted from Bailey et al. 1988).

Grazing Regime (Year started)	Average Percent Use (%)	AUM's[1] Grazed	Period Grazed
Light June (1973)	32	8	June 1-30
Heavy June (1973)	61	24	June 1-30
Heavy Continuous (1976)	75	24	June 1- Sept 15
Heavy Autumn (1973)	67	24	Sept. 15 - Oct. 15
Light Autumn (1973)	37	8	Sept. 15 - Oct. 15

[1] AUM = Animal unit month

(2 X 10 m). For the season of defoliation experiment there was a control, burnt control, May, June, July, August, September, and October annual defoliation treatments. For the frequency of defoliation experiment there was a control, burnt control, and treatments of one, two, four and eight cuts per growing season. A schema of the randomized block design is shown in Figure 2.2.

GEOLOGY

This area is located in the 'Interior Plains' physiographic region of Canada, one of the seven major physiographic regions of Canada (Clayton et al. 1977). This physiographic region stretches south from the Arctic ocean and east from the Rocky Mountain range to the western edge of the Canadian Shield. It consists of younger sedimentary rocks which form a ring around the massive older surface of the Canadian shield. The underlying geology and relief of the interior plains is of sedimentary rocks which lie in nearly horizontal beds creating a vast plain which gently slopes from west to east. These sedimentary rocks consist of limestone, sandstone, and shale. The effect of alternating semiarid and subhumid periods and the associated fluvial erosion during the Tertiary time period resulted in deposits of sand and gravel across the Interior plains and the carving out of uplands and lowlands.

Following the long period of preglacial erosion during the tertiary period, the Interior Plains were subjected to the effects of

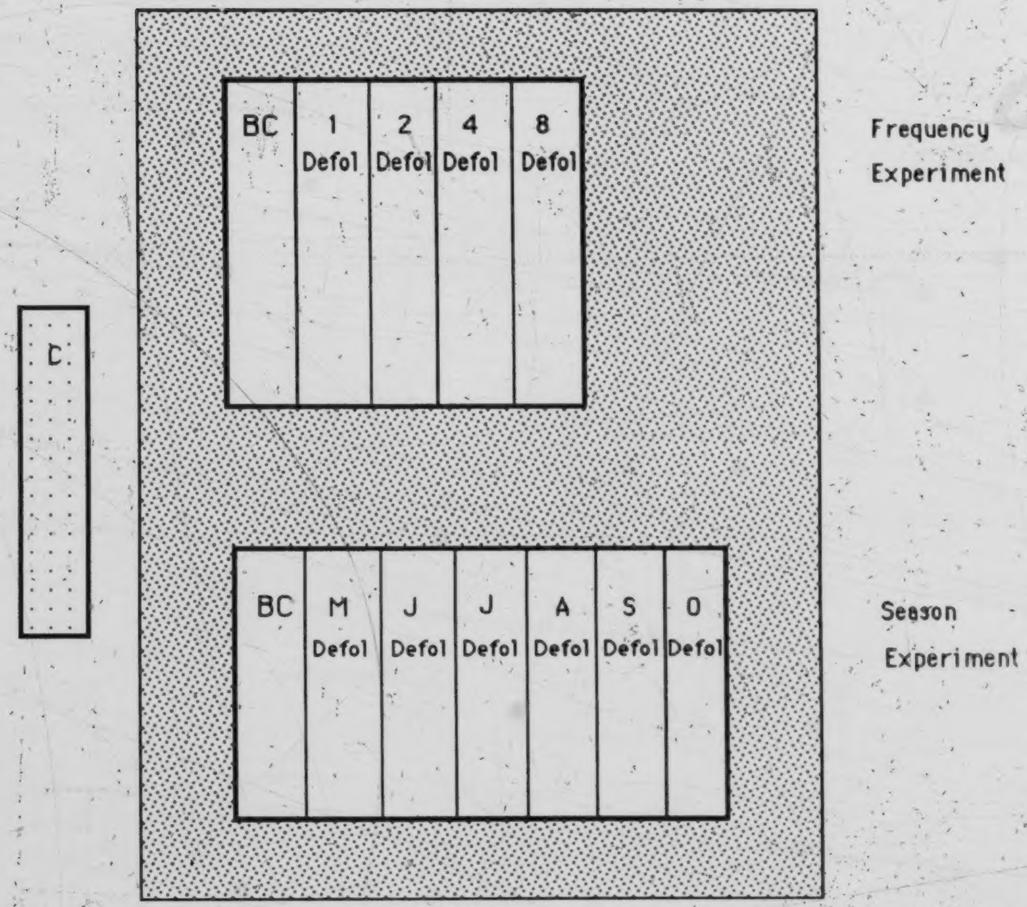
BC
1 Defol
2 Defol
4 Defol
8 Defol
Frequency Experiment
C
BC
M Defol
J Defol
J Defol
A Defol
S Defol
O Defol
Season Experiment

Figure 2.2 Schema of a randomized block for season of defoliation and frequency of defoliation experiments. Ten blocks were used in each experiment

repeated glaciation, as was most of Canada, during the quaternary period (Clayton et al. 1977). This repeated process of glaciation has been the dominant geological process affecting the present pattern of parent ground material and landform features which underlie the composition and distribution of prairie soils. The general effect of each glaciation was the deposition and incorporation of the glacial load with the underlying shales. The pattern of these surficial deposits ranges from flat lacustrine clay basins to gently rolling till plains to rough, undulating and hummocky end moraine deposits.

Drainage from the Interior Plains physiographic region is either north to the Arctic Ocean, northeast to Hudson Bay, or south to the Gulf of Mexico (Clayton et al. 1977). Drainage for the eastern portion of the county of Beaver flows northeast through the North Saskatchewan and Battle River drainage systems to the Hudson Bay.

The landform of Section 28 is morainal hummocky with the hummocks being characterized by short steep slopes and interspersed with numerous pothole lakes (Howitt 1988). This topography is frequently called "knob and kettle". The hummocky topography of the Viking Upland district is the result of the disintegration and melting of a stagnant ice mass as opposed to a retreating glacier. The district is covered by a yellowish-brown till which consists of approximately equal parts of sand, silt and clay, and a gravel content of less than 10%. Several lakes: Thomas, Vernon, Hattie, Camp, and Carrier run north to south through the district in association with a meltwater channel. There are sand

and gravel deposits in and around the study area due to glaciofluvial deposits associated with the sorting of the till by the meltwater from the glacier ice. A major example of these deposits is the county-operated gravel pit on the University Ranch about 5 km southeast of Section 28. There are no major creeks in the district. The underlying bedrock formation below the Viking Upland district is the Belly River Formation which is an upper cretaceous sediment consisting of sandstone, mudstones, siltstones, and concretionary iron stone beds which were deposited in a non-marine environment.

SOILS

The Chernozemic-Gleysolic soil association is the predominant soil association across the landscapes of Section 28 and the University of Alberta ranch (Scheffler 1976). Scheffler (1976) found that Chernozemic and Gleysolic soils accounted for 96% of the soils in the *Populus tremuloides* groves sampled on the University of Alberta ranch. The remaining 4% were Luvisolic soils. A common soil-plant community association on Section 28 as reported by Scheffler (1976) and Wheeler (1976) is shown in Figure 2.3. The Solonetzic soils are not a reported component of the soils of the University ranch or of Section 28 although many of the sloughs are saline.

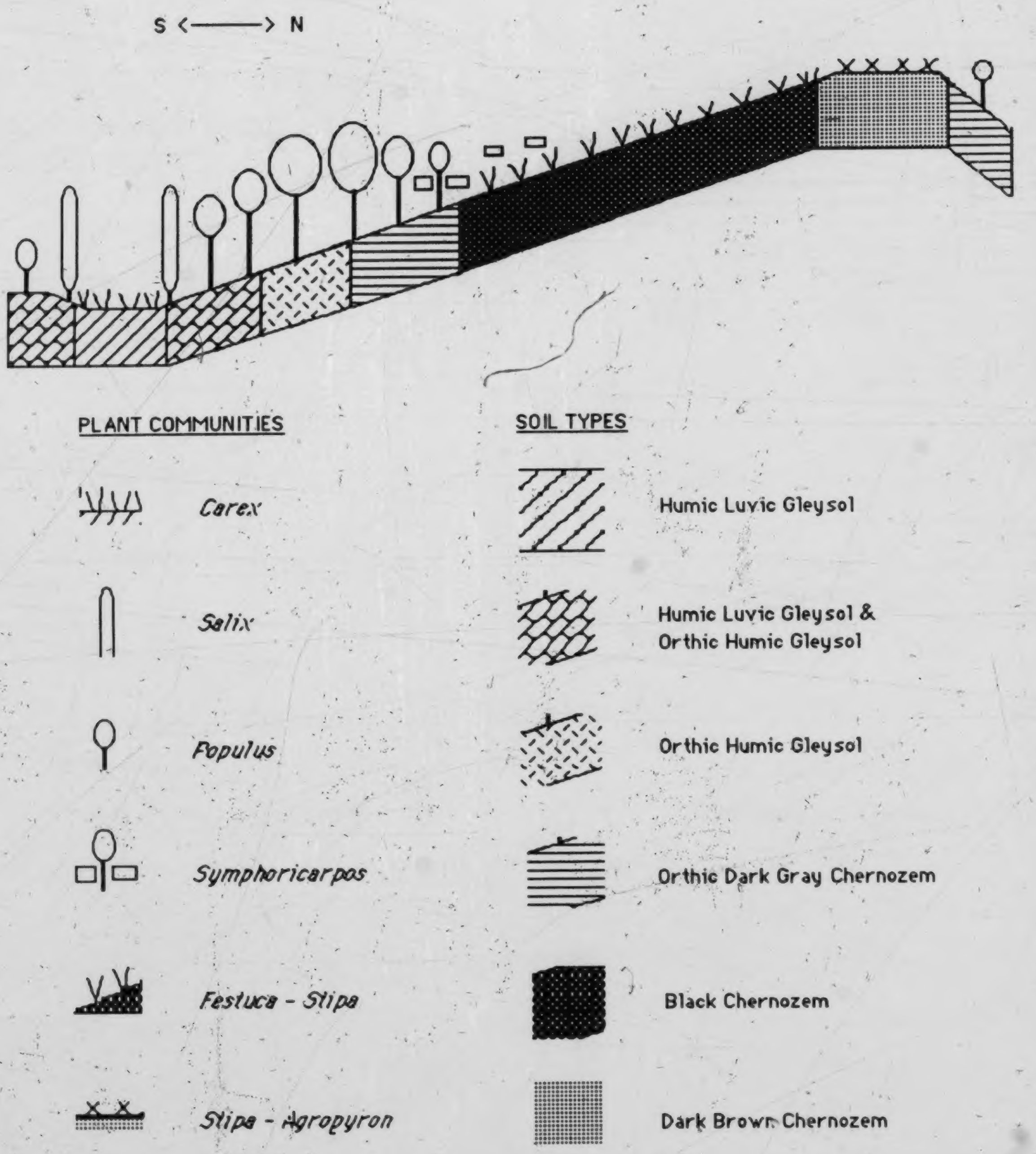
S <——> N
PLANT COMMUNITIES
Carex
Salix
Populus
Symphoricarpos
Festuca - Stipa
Stipa - Agropyron
SOIL TYPES
Humic Luvic Gleysol
Humic Luvic Gleysol & Orthic Humic Gleysol
Orthic Humic Gleysol
Orthic Dark Gray Chernozem
Black Chernozem
Dark Brown Chernozem

Figure 2.3 A common soil-plant community association on southern exposures in Section 28. Adapted from Scheffler (1976) and Wheeler (1976).

The Chernozemic regions are characterized by black surface horizons which are thought to reflect the dominance of grassland vegetation and comparatively warm climates in the development of these soils (Howitt 1988). The Chernozemic soils are either Black or Dark Gray and are typically found under grassland or transitional grassland-woodland vegetation. The B and C horizons are characterized by high base saturation. The Black great group has an Ah horizon usually > 10 cm and a color of dark gray to black. The Dark Gray great group has an Ah with light gray spots or bands and usually a lighter colored Ahe horizon. The Ahe horizon reflects some degree of eluviation which is often associated with the invasion of *Populus* vegetation into grassland areas. Dark Brown Chernozems are not reported by Howitt (1988) but are reported by Wheeler (1976) on the crests of the morainal hummocks.

Elnora is a thin, well drained Orthic Black Chernozem and the dominant soil on Section 28 (Howitt 1988). The soils of this area have been called zonally normal shallow black soils (Wyatt et al. 1944). Typical profiles have a black, loamy surface horizon 10-15 cm thick underlain by a yellow brown, weakly to moderately prismatic B horizon (Howitt 1988). Unaltered parent material is encountered at 40-60 cm which is fine loamy to fine clayey till with less than 5% coarse fragments. It is 8 - 30 m thick and moderately calcareous. Lenses of sand and gravel are common. Rainfall enters the soil by infiltration but surface runoff may occur on steep slopes where erosion potential is high.

The Humic Gleysol great group of the Gleysolic order is found on Section 28 of the University Ranch (Scheffler 1976, Howitt 1988). This great group is characterized by a thick Ah ≥ 10 cm and no Bt horizon (CSSC 1978). The mineral horizons are strongly gleyed and prominent mottles may be present reflecting a high or fluctuating water table. Organic surface horizons may be up to 60 cm thick and dull grayish colors are characteristic throughout the profile (Howitt 1988). Poor drainage is a dominant factor in the development of the Gleysolic soils and they frequently occur in lowland depressions and around potholes in association with other upland soil orders.

The Solonetzic soils are characterized by Solonetzic B horizons and saline parent material and have developed under variable drainage and vegetation conditions. The Solonetzic soils occur primarily between the towns of Tofield and Viking in the County of Beaver to the west of Section 28 (Howitt 1988). They are reported as possible inclusions in soil associations such as the Elnora (EOR) mapping units which are reported on Section 28. Other workers (Wheeler 1976, Scheffler 1976) have not reported Solonetzic soils in Section 28 although some of the sloughs are saline.

Despite the extensive presence of *Populus* forest cover, the fact that Luvisolic soils are present in such a small percentage on Section 28 (Scheffler 1976) suggests that the soils of this area developed originally under a predominantly grassland vegetation rather than under forest cover (Pettapiece 1969). While this is probably true for the upland grass and shrub communities with Black and Dark Brown Chernozemic soils, it may not be true for the soils of the *Populus* communities. Of the 20 soil types identified by Scheffler (1976) in the *Populus* communities, the three most common were Humic Luvic Gleysol (26%) (which Scheffler (1976) called Humic Eluviated Gleysol), Orthic Dark Gray Chernozem (18%), and Orthic Humic Gleysol (17%). Both gleysolic soils are a function of a high or fluctuating water table. This is consistent with their low slope position. The Humic great group classification is indicative of a thick Ah horizon (≥ 10 cm) reflecting a lush sedge, grass, moss and/or forest vegetation (CSSC 1978).

The low slope *Carex* and *Salix* plant communities are mesophytic, reflecting the higher moisture status of the Gleysolic soils. The oldest portion of the *Populus* community is located on the lower slope edge of the Orthic Dark Gray Chernozem (Scheffler 1976). This could reflect an invasion of *Populus* and the subsequent degradation of the Black Chernozem to a Dark Gray Chernozem given the acidic nature of the *Populus* litter. Alternately it is possible that this parkland forest vegetation and the associated soil developed simultaneously as an adjunct to the upland shrub and grassland communities (Pawluk 1982). Sanborn and Pawluk (1983) suggest the possibility that Black Chernozemic soils, as defined by the Canadian System of Soil Classification, could have developed under the influence of forest cover. Alternating forest and grassland communities in these lower slope positions from influences such as fire could lead to the formation of a Dark Gray Chernozem (Pawluk 1982). Scheffler (1976) interpreted the development of the Dark Gray Chernozems on this landscape as due to *Populus* invasion since the average age of the oldest trees was only 22 years. The assumption was made that degradation of the Black Chernozems to Dark Gray Chernozems could have occurred in this time period. Scheffler (1976) did not specifically report any podzolization effect in the degradation of Black Chernozems to Dark Gray as reported by Dormaar and Lutwick (1966) with the invasion of *Populus tremuloides* into grasslands in the *Festuca campestris-Populus tremuloides* transition zone of southwestern Alberta.

Soil moisture across the Gleysolic-Chernozemic soil association is influenced by vegetation type in addition to topography. Wheeler (1976) reported the shrubland community soils to be drier than the grassland community soils. This was presumably related to a higher rate of transpiration by the shrubs compared to the grasses. The validity of the observation, however, would be dependent on the time of year at which it was made, as Scheffler (1976) reported a changing differential in soil moisture between the communities as the spring and summer passed. The grasslands had their lowest soil moisture in June, which is normally the highest rainfall period in the year (Figure 2.4), whereas the treed communities had considerably higher soil moisture due to slower snow melt and possibly a slower initiation of spring growth. By August, however, soil moisture under the aspen forest was less than in the grassland; the high rate of transpiration by the woody species appeared to slowly dry up the sloughs (Scheffler 1976). If the woody vegetation was pumping the sloughs dry, which otherwise might remain wet throughout the summer, there could be an increased prominence of mottles in the Gleysolic soils given the pronounced alternation between wet (reducing) and dry (oxidizing) conditions. This would be in contrast for soils with a more uniform gleyed effect with less mottling where continual wet (reducing) conditions were prevalent.

Wheeler (1976) did not find any significant differences in major soil nutrients or in soil pH between the shrub and grassland communities. Scheffler (1976) found that potassium and phosphorus levels were significantly increased with lower slope positions. The potassium increase was attributed to downslope leaching by water and/or increased potassium release by the leaf fall of the lower slope *Salix* plant communities. The low phosphorus in the upper slope positions was also attributed, in part, to the presence of free lime in the upper slope positions. Scheffler (1976) reported overall significant decreases in soil pH in moving from the upper to lower slope positions. Some variation in the lower slope pH was observed at the break of the slope which was attributed to recarbonation associated with fluctuating water tables moving over alkaline parent material. The overall trend to lower pH with lower slope position was attributed to the increased leaching of cations with lower slope position.

Five soil pits were dug in the study site on the west side of Carrier Lake. The soils were either Orthic or Solonetzic Black Chernozems (R. W. Howitt, personal communication, October 1987). The Ah horizons were 8 to 14 cm in depth with pH ranging between 5.7 and 6.2, with a loam or clay loam texture. In three of the soil pits there was an Ahe or Ae horizon of 7 to 16 cm depth with pH ranging from 5.7 to 6.1 with either loam, clay loam or sandy clay loam textures. The B horizons ranged from 19 to 46 cm in depth with pH ranging from 6.7 to 8.4 with either loam, clay loam or sandy clay loam textures. The Ck horizon started at a depth ranging from 40 to 61 cm with a pH between 8.1 and 8.4 with either clay loam or sandy clay loam textures.

CLIMATE

Climate can be argued to be the most important factor shaping the character and distribution cf ecosytems (Ecoregions Working Group 1989). Climate involves the long-term pattern of temperature, energy and moisture relationships of the biosphere for a given place (Clayton et al. 1977). The Ecoregions Working Group (1989) of Environment Canada has divided Canada into ten ecoclimatic provinces based on climatic patterns. Their approach is similar to the zonobiome approach developed in Germany (Walter 1985) for classifying vegetation distribution based on climate.

The study area falls into the Grassland Ecoclimatic Province of Canada (Ecoregions Working Group 1989). The Grassland Ecoclimatic Province is divided into the Transitional Grassland Region, Subhumid Grassland Region and the Arid Grassland Region. The Arid Grassland Region corresponds to the Mixed Prairie Association and the Subhumid and Arid Grassland Regions to the Fescue prairie association as proposed by Coupland (1961). The distinction between the Transitional Grassland Region and the Subhumid Grassland Region for the Fescue prairie association would appear to correspond to the geographic distributions for *Festuca hallii* and *Festuca campestris* respectively (Pavlick and Looman 1984, Harms 1985).

The study site also falls into the Parkland climate region according to Alberta Agriculture (Dzikowski and Heywood 1990). Records from the University of Alberta ranch headquarters indicated an average annual temperature of 1.9° C and a total average annual precipitation of 432 mm of which 323 mm, or 75%, falls mostly as rain between April and September (Atmospheric Environment Services 1985-1987). The frost free period (i.e. consecutive days > 0° C) is about 100. The date of the last spring frost (0° C) is about May 31 and the first fall frost (0° C) is during the first week of September. The start of the growing season is between April 21st and 26th with the end of the growing season between October 5th and 10th with the average length of the growing season between 165 and 170 days (average daily temperature > 5° C). Elevation is approximately 700 m above sea level.

A climate diagram of the air temperature and precipitation for Kinsella for the period of 1962 -1980 inclusive (Figure 2.4) is similar to the cold-temperate Boreal climate of the mixed-forest zone and boreal zone of northern Europe and Siberia (Walter 1985).

It is important to note that, in long-term averages, precipitation exceeds potential evapotranspiration only during June (Figure 2.5). Potential evapotranspiration exceeds precipitation during the rest of the growing season and is particularly pronounced during May, August and September. The excess of precipitation over potential evapotranspiration for June combined with it having the third highest average monthly temperature and the greatest daylengths of the year together suggest that it could be a critical month in the growth cycles of plant species in the *Festuca-Stipa* grasslands.

The monthly precipitation and temperature patterns for 1985 to 1987 with reference to the long-term monthly averages are given in Tables 2.2, 2.3, and 2.4. The two critical years for the results reported in this thesis are 1986 and 1987. While both years were drier than normal for May and June, this trend was particularly pronounced in 1987 with June of that year having only 43% of the monthly long-term average precipitation (Table 2.2) and 63% of the long-term average for accumulated precipitation (Table 2.3). July and September in 1986 had precipitation amounts which

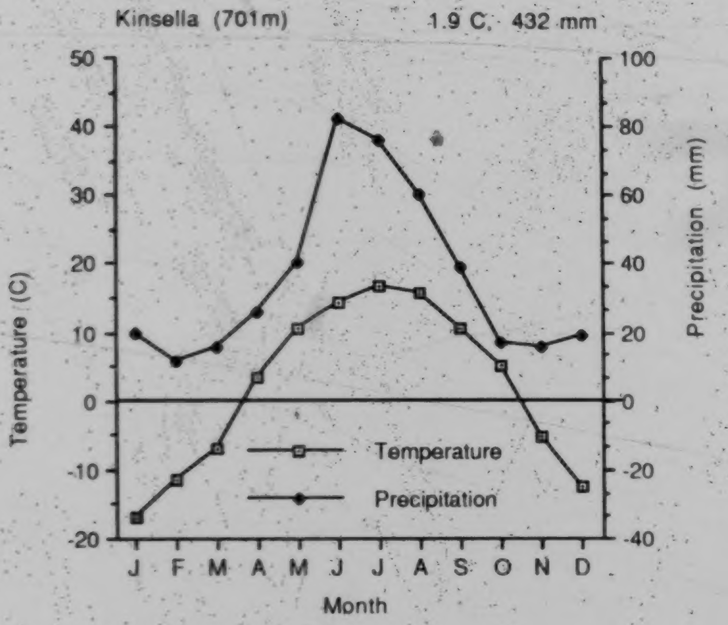

Figure 2.4 Climate diagram for long-term (1962-1980) temperature and precipitation at Kinsella, Alberta (adapted from Atmospheric Environment Services 1985-1987).

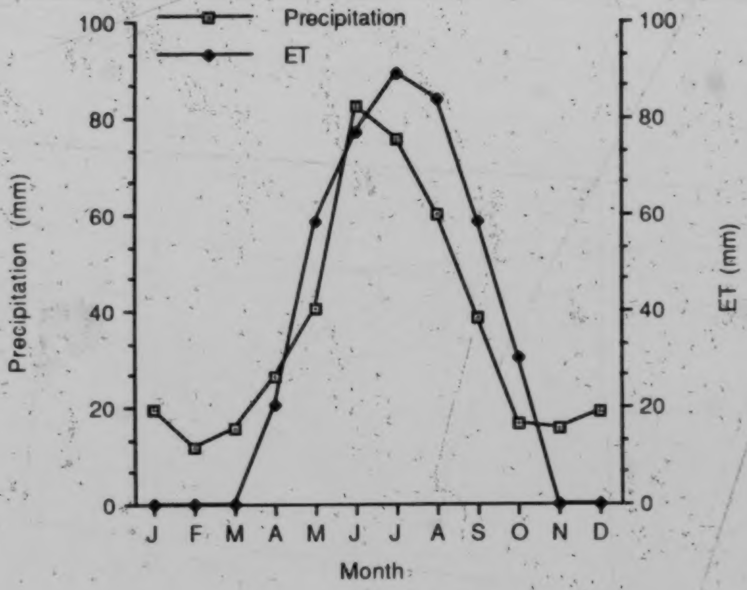

Figure 2.5 Long-term (1962-1980) precipitation and potential evapotranspiration (ET) for Kinsella, Alberta (adapted from Atmospheric Environment Services 1985-1987).

Table 2.2 Monthly precipitation, monthly precipitation as a percentage of the long-term (1962-1980) average, and 1987 precipitation as a percentage of the 1986 precipitation at the University of Alberta ranch headquarters, Kinsella, Alberta (modified from Atmospheric Environmental Services 1985-1987).

	Precipitation (mm)				Precipitation as % of long-term average (%)			1987 as a % of 1986 (%)
Month	Long-term average	1985	1986	1987	1985	1986	1987	
Jan	24.1	21.8	12.6	1.3	90	52	5	10
Feb	16.2	10.0	8.0	18.4	62	49	114	230
Mar	17.6	3.2	23.2	15.7	18	132	89	68
Apr	17.8	23.8	17.8	28.6	134	100	161	161
May	45.0	59.0	24.7	24.8	131	55	55	100
Jun	77.9	56.2	60.4	33.8	72	78	43	56
Jul	86.4	22.0	115.5	83.9	25	134	97	73
Aug	58.5	70.5	20.8	79.8	121	36	136	384
Sep	37.3	32.6	62.7	31.0	87	168	83	49
Oct	15.3	46.0	16.0	11.0	301	105	72	69
Nov	15.1	14.9	24.0	6.8	99	159	45	28
Dec	20.3	36.2	9.0	9.0	178	44	44	100

Table 2.3 Accumulated monthly precipitation, accumulated monthly precipitation as a percentage of the long-term (1962-1980) average, and 1987 accumulated precipitation as a percentage of 1986 accumulated precipitation at the University of Alberta ranch headquarters, Kinsella, Alberta (modified from Atmospheric Environmental Services 1985-1987).

	Accumulated precipitation (mm)				Accumulated precipitation as % of long-term average (%)			1987 as a % of 1986 (%)
Month	Long-term average	1985	1986	1987	1985	1986	1987	
Jan	24.1	21.8	12.6	1.3	90	52	5	10
Feb	40.3	31.8	20.6	19.7	79	51	49	96
Mar	57.9	35.0	43.8	35.4	60	76	61	81
Apr	75.7	58.8	61.6	64.0	78	81	85	104
May	120.7	117.8	86.3	88.8	98	71	74	103
Jun	198.6	174.0	146.7	122.6	88	74	62	84
Jul	285.0	196.0	262.2	206.5	69	92	72	79
Aug	343.5	266.5	383.0	286.3	78	82	83	101
Sep	380.8	299.1	345.7	317.3	79	91	83	92
Oct	396.1	345.1	361.7	328.3	87	91	83	91
Nov	411.2	360.0	385.7	335.1	88	94	81	87
Dec	431.5	396.2	394.7	344.1	92	91	80	87

Table 2.4 Average monthly temperature and monthly difference from the long-term (1962-1980) monthly average temperature at the University of Alberta ranch headquarters, Kinsella, Alberta (modified from Atmospheric Environmental Services 1985-1987).

	Average monthly temperature (° C)				Monthly difference from long-term monthly average (° C)		
Month	Long-term Average	1985	1986	1987	1985	1986	1987
Jan	-16.9	-10.7	-6.6	-7.1	6.2	10.3	9.8
Feb	-11.4	-13.5	-14.0	-5.4	-2.1	-2.6	6.0
Mar	-6.9	-2.3	0.1	-6.0	4.6	7.0	0.9
Apr	3.2	5.1	3.6	7.1	1.9	0.4	3.9
May	10.4	12.1	11.9	12.3	1.7	1.5	1.9
Jun	14.2	12.5	14.9	17.0	-1.7	0.7	2.8
Jul	16.7	17.9	15.0	16.9	1.2	-1.7	0.2
Aug	15.6	14.5	16.3	13.2	-1.1	0.7	-2.4
Sep	10.4	6.9	8.5	13.3	-3.5	-1.9	2.9
Oct	4.9	3.6	6.8	5.5	-1.3	1.9	0.6
Nov	-5.2	-14.2	-9.3	0.2	-9.0	-4.1	5.4
Dec	-12.4	-7.8	-6.8	-6.0	4.6	5.6	6.4

were 34% and 68% higher than the long-term monthly averages. This raised the accumulated precipitation for July and September to 92% and 91% of the long-term average for 1986, versus 72% and 83% in 1987. The accumulated precipitation on a monthly basis during the 1986 growing season was less than normal by 9% to 29% and during the 1987 growing season it was less than normal by 17% to 38% (Table 2.2). With the exception of August, all the growing season monthly temperatures were higher in 1987 than 1986 (Table 2.4).

VEGETATION

The study area is on the northern edge of the grassland ecoclimatic province in Canada and is a transitional zone between the more arid prairie to the south and the moister boreal forest to the north (Ecoregions Working Group 1989). Undisturbed areas are characterized by a mosaic of *Populus tremuloides* groves and *Festuca hallii* grasslands. *Populus tremuloides* groves occur on the moister sites with shrub and grassland communities on the drier sites. Shrub communities are dominated by *Amelanchier alnifolia*, *Elaeagnus commutata*, *Rosa acicularis*, *Rosa woodsii* and *Symphoricarpos occidentalis*. *Festuca hallii* dominates open undisturbed sites but *Stipa curtiseta* co-dominates on grazed sites (Wheeler 1976). Other grasses characteristic of the area depending on site aspect, moisture and disturbance include *Agropyron smithii*, *Agropyron dasystachyum*, *Bouteloua gracilis*, *Koeleria macrantha*, *Helictotrichon hookeri*, and *Poa pratensis*. *Solidago missouriensis* and *Thermopsis rhombifolia* were characteristic forb increasers on disturbed sites (Bailey et al. 1988). *Artemisia frigida* was a characteristic woody increaser on disturbed sites.

The topography of the area as noted earlier is a hummocky moraine. The type of vegetation growing in this region appears to be affected by soil moisture, slope position and aspect. Work done by Scheffler (1976) and Wheeler (1976) would suggest the sequence of native plant communities moving up a southerly slope of a hummock as illustrated in Figure 2.3. In the mesic slough bottom, or around its edges if it is a site of permanently standing water, would be a *Carex* community. Ringing the slough would be a grove of *Salix* trees. Surrounding the *Salix* ring on the outside would be a grove of *Populus tremuloides* trees. These trees varied in age with the oldest generally being in the middle of the grove and the younger trees feathering out to the upper and lower edges (Scheffler 1976). Between the *Populus* community and the grassland, *Symphoricarpos* and then a transitional *Symphoricarpos-Festuca* community would be found. Frequently mixed in with these communities is *Elaeagnus commutata*. At this point the grassland proper starts with the *Festuca-Stipa* community moving up the slope to the crest of the hummock. The grassland may then shift to a *Stipa-Festuca* community before changing to *Stipa-Agropyron* community on the crown of the hummock. The above description is more detailed than Figure 2.3 which does not detail the transitional plant communities noted above. The north facing slope frequently would be a shrub community or *Populus* community because of the cooler and more mesic conditions. The higher moisture conditions on the northern slope are often related to a higher level of winter snow accumulation (Strong and Leggat 1981). This is a direct influence of aspect as it affects microclimate and thereby alters the local vegetation and soils. In saline lowlands, salt grass meadows replace the sedge meadows.

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III. GROWTH AND FORAGE QUALITY OF PLAINS ROUGH FESCUE IN A *FESTUCA-STIPA* GRASSLAND IN CENTRAL ALBERTA

INTRODUCTION

Establishment of an optimum defoliation regime for a grassland is contingent upon an understanding of the basic biology, growth and forage quality cycles of its key species when that species is not subjected to defoliation stress (Tainton 1981). *Festuca hallii* (Vasey) Piper[1] is the key species in the *Festuca-Stipa* grasslands of central Alberta (Pavlick and Looman 1984, Wroe et al. 1988). This native grassland has been shown to have forage production that was equal to, or better than, the forage production of *Bromus inermis-Festuca rubra* swards in the absence of a legume at the University of Alberta Ranch near Kinsella, Alberta (Bailey et al. 1980).

There has been some confusion in both the taxonomy and nomenclature of the North American rough fescues (Pavlick and Looman 1984, Harms 1985). Historically, the key species in the *Festuca-Stipa* grasslands of the aspen parkland of central Alberta and the *Festuca-Danthonia* grasslands of the Rocky Mountain foothills of south-western Alberta, has been called *Festuca scabrella* (Moss 1983). The rough fescues of these two regions have been commonly distinguished as the plains rough fescue and foothills rough fescue, respectively. The species nomenclature for the North American rough fescues as proposed by Pavlick and Looman (1984) will be followed in this paper with the plains rough fescue identified as *Festuca hallii* (Vasey) Piper and the foothills rough fescue as *Festuca campestris* Rydb..

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[1] Scientific nomenclature follows Moss (1983) except where a different authority is cited in the text.

With the exception of a study by Stout et al. (1981), no research has been published on the growth cycle and phenology of the rough fescues in Western Canada in the last decade. Pidgen (1953), and Johnston and Bezeau (1962), conducted survey studies of forage quality for several forage species found in western Canada which included *Festuca campestris* or *Festuca hallii*. Both studies provided some forage quality information at four, or five, generalized growth stages. Dragt and Havstad (1987) evaluated the winter, or weathered, chemical composition of *Festuca hallii* which was sampled in March after being grazed at different growth stages during the previous growing season. None of these studies provided detailed information on the forage growth cycle, forage quality cycle, or phenology of *Festuca hallii* or *Festuca campestris* during the growing season. The growing season pattern for soluble carbohydrate storage in a species has been associated with its grazing tolerance (Menke and Trlica 1981). No research has been published on the soluble carbohydrate storage pattern of *Festuca hallii* or *Festuca campestris* through their growing seasons.

The sensitivity of *Festuca hallii* to defoliation has been noted since the early survey work (Moss and Campbell 1947). Therefore there is a need to establish information regarding the growth patterns of this plant in the absence of defoliation in order to better understand its sensitivity to defoliation. The purpose of this study was to establish information on the growth cycle, forage quality cycle, and pattern of soluble carbohydrate storage for *Festuca hallii* within a *Festuca-Stipa* grassland in central Alberta in the absence of defoliation stress during the 1987 growing season.

MATERIALS AND METHODS

Study Area and Experimental Design

The study area (53°N, 112°W) was located on Section 28 of the University of Alberta's research ranch approximately 150 km southeast of Edmonton, Alberta. A cold-temperate Boreal climate prevails (Walter 1979). The average annual temperature is 1.9° C. Total average annual precipitation is 432 mm of which 323 mm or 75% occurs between April and September. Elevation is approximately 700 m above sea level. The grassland soils are predominantly thin Orthic Black Chernozems (Howitt 1988). The grazing season is traditionally from May to December depending on the species being grazed and on annual variations in precipitation and snowfall patterns.

The study area is on the northern edge of the grassland ecoclimatic province in Canada. It is a transitional zone between the more arid prairie to the south and the moister boreal forest to the north (Ecoregions Working Group 1989). Undisturbed areas are characterized by a mosaic of *Populus tremuloides* groves and *Festuca hallii* grasslands. Groves of trees occur on the moister sites with shrub and grassland communities on the drier sites. Shrub communities are dominated by *Amelanchier alnifolia*, *Elaeagnus commutata*, *Rosa acicularis*, *Rosa woodsii* and *Symphoricarpos occidentalis*. *Festuca hallii* dominates open undisturbed sites but *Stipa curtiseta* co-dominates on grazed sites (Wheeler 1976). Recent research indicates that *Festuca hallii* is also the dominant in autumn grazed areas (Bailey et al. 1988). Other grasses characteristic of the area depending on site, aspect, moisture and disturbance include; *Agropyron smithii*, *Agropyron trachycaulum*, *Agrostris scabra*, *Bouteloua gracilis*, *Festuca saximontana*, *Koeleria macrantha*, *Helictotrichon hookeri* and *Poa pratensis*. *Artemisia frigida* was a characteristic woody increaser on disturbed sites.

The specific study site was a 22.5 ha wedge of the aspen parkland mosaic consisting of grassland (3.4 ha or 21%) and aspen forest and shrubs (17.8 ha or 79%) running north to south on the east side of Carrier Lake. This site had not been grazed for about 25 years. At the beginning of May, 1985, ten blocks (20 X 40 m) within the grassland area were burnt to remove the heavy accumulation of litter. Two control plots (2 X 10 m) within each burnt block were established. On April 24th, 1987, a section (1 X 2 m) of each control plot was mowed to a 3-cm height with a rotary mower.

Within each block, one randomly chosen control plot was assigned for collecting aboveground dry matter yield (DMY) and phenology data and the other was assigned for collecting soil cores for determination of stem base weights, stem base total nonstructural carbohydrate percentage (TNC%), stem base TNC pool and root weights. Each of the mowed sections was subdivided into 10 subplots (40 X 50 cm). For aboveground biomass and phenology data, nine subplots were randomly assigned for sequential clipping dates, while one subplot was randomly assigned to monitor the phenology of *Festuca hallii* on each of the sampling dates. The growth cycle and phenology sampling dates (Julian date) were: May 6 (126), May 22 (142), June 4 (155), June 17 (168), July 5 (186), July 16 (197), Aug 4 (216), Sept 4 (247), and Oct 4 (277). The same procedure was repeated for assignment of the ten subplots for sequential core sampling for the stem base and root samples, with the exception, that sampling dates began with April 24 (114). After April 24th (114), the sampling dates were the same as the phenology and aboveground growth data collection dates.

Dry Matter Yield and Sward Composition

The aboveground biomass was clipped from three 10 X 40 cm quadrats in each subplot on each sampling date. *Festuca hallii*, other grasses and grass-like plants, and forbs combined with woody species were separated at the time of clipping. These samples were dried to a constant weight at 65° C, and aboveground dry matter yield (DMY) was determined by taking the average DMY of the three 10 X 40 cm quadrats for each block for each sampling date. Sward composition (DM%) was determined on the basis of these DM yields for each date.

Leaf Height and Senescence

The extended leaf height was measured on each sampling date for three randomly chosen tillers from within the phenology subplot by using a straight ruler placed vertical to the soil surface (Rhodes 1981). From June 4th (155) when the leaf tips began to senesce (brown), the extended height of the green portion of the leaf was also measured.

Growth Stage

The growth stage was noted on each sampling date for three randomly chosen tillers in the phenology subplot, using the growth stage terminology developed by Metcalfe (1973).

Forage Quality of *Festuca hallii*

The quantity of forage for the first two sampling dates from the ten individual blocks was inadequate for both standard laboratory procedures and NMR analysis. Therefore, the samples from the ten blocks were randomly mixed and bulked to two blocks to provide enough forage material for each sampling date. Standard laboratory analysis through the University of Alberta's Department of Animal Science included crude protein (CP), neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL). Hemicellulose (HC) and cellulose (CL) were calculated as HC=NDF-ADF and CL=ADF-ADL (Goering and Van Soest 1970). Qualitative organic analysis of the protein, lipid and cellulose-lignin components of *Festuca hallii* at different stages of maturity was performed by nuclear magnetic resonance (NMR) analysis through the Alberta Research Council, Edmonton (Efloson et al. 1984).

Stem Base Weight, TNC (%), TNC Pool and Root Weight

The *Festuca hallii* stem base weight, total nonstructural carbohydrate percentage (TNC (%)) and TNC pool were determined as follows. The stem base refers to the part of the *Festuca hallii* plants between the interface of the roots and the stembase and the 2-cm stubble height. Two 7.0 cm diameter by 7.5 cm deep cores were extracted from each block for each sampling date. The cores were immediately placed in plastic bags, sealed, transported to a freezer, and frozen within thirty-six hours of removal from the ground. Prior to analysis, the samples were thawed overnight at room temperature. The foliage was trimmed to 2 cm above the soil surface. The cores were washed and broken up under cool tap water over a 2 mm screen to remove the soil from the roots. During the washing process, the non-*Festuca hallii* species were separated and discarded. The *Festuca hallii* stem bases and roots were separated by trimming 2 to 4 mm below the interface of the stem base and roots. Rhizomes were retained with the stem bases. The stem base and root samples were oven dried at 65° C to a constant weight and then weighed. The stem base samples were ground using a Udy cyclone mill (1 mm screen). The ground stem base samples were frozen, awaiting later analysis for TNC. Root samples were weighed and discarded.

Prior to TNC analysis, the stem base samples were removed from the freezer, dried overnight to a constant weight at 65° C, and then stored in a desiccator. Stem base TNC (%) was determined with an acid hydrolysis technique. The technique was adapted from Smith (1981) in consultation with M. J. Trlica (personal communication, February 1987) and J. H. Richards (personal communication, May 1987). Duplicate 100-mg stem base samples from each block for each sampling date were refluxed in 6 ml of 0.2N H_2SO_4 for one hour in a marble capped 25 X 200 mm test tube in a covered boiling water bath. The amount of fructosan (mg) in each sample was subsequently determined by the Schaeffer Somogyi copper-iodometric titration technique as outlined by Smith (1981).

The stem base TNC pool was determined by multiplying the stem base weight by the TNC percentage to provide an estimate of the TNC pool (g m^{-2}).

Statistical Analysis

As sampling dates were unevenly spaced for the parameters measured, stepwise polynomial regression was used to determine curves with the best fit as a function of Julian date (Zar 1974, Steel and Torrie 1980). The polynomial equation was selected when the two consecutively higher order polynomials did not provide a significantly higher coefficient of determination, and the form of the equation was consistent with the established biology of the parameter being measured.

RESULTS

Dry Matter Yield

Aboveground DMY for the *Festuca-Stipa* sward and the sward components of *Festuca hallii*, other grasses and grass-like plants, and forbs and woody species for 1987 is shown in Figure 3.1. Growth started about April 24th (Julian day=114) and the final collection was made October 2nd (275). Aboveground DMY peaked in September for all three sward components. During late June there was a decline in the DMY for the forbs and woody species which was most likely associated with the low June precipitation of only 33.8 mm (43 % of the long term monthly average). For *Festuca hallii* and the other grasses and grass-like components of the sward there was no decline in DMY during the dry June period suggesting that the grasses and the grass-like plants were more drought tolerant than

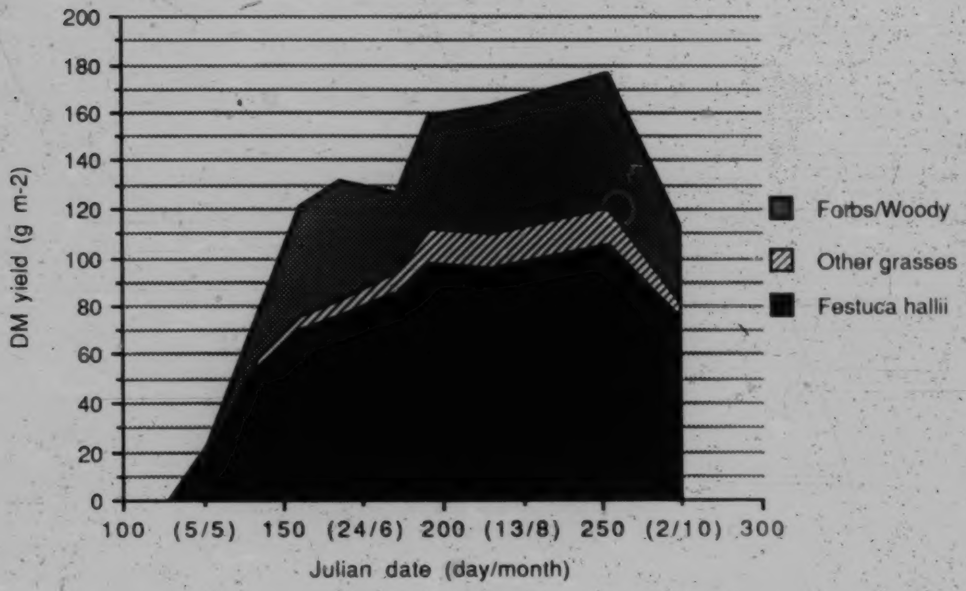

Figure 3.1 Sward aboveground dry matter (DM) yield of *Festuca hallii*, other grasses and grass-like species, and forbs and woody species through the 1987 growing season by sampling date.

the forbs and woody species. Precipitation occurred in early July and all three sward components responded with increased rates of DM production. This was most notable for the forbs and woody species.

Curve fitting using stepwise polynomial regressions yielded a quadratic regression ($P<0.001$, $R^2=0.68$) for the sward aboveground DMY (Table 3.1, Figures 3.1, 3.2). This regression suggested that the period of most rapid sward growth was from April 24th (114) to June 17th (168) with growth rate declining through July and aboveground DMY peaking about August 6th (218).

For the *Festuca hallii* aboveground DMY, curve fitting using stepwise polynomial regressions also yielded a quadratic regression ($P<0.001$, $R^2=0.57$) (Table 3.1, Figure 3.3). This regression suggests that the period of most rapid *Festuca hallii* growth was from April 24th (114) to June 4th (155) with growth rate declining through late June and July and aboveground DMY peaking about August 9th (221).

In contrast to the two previous regressions, curve fitting using stepwise polynomial regressions yielded a cubic regression ($P<0.001$, $R^2=0.26$) for aboveground DMY of the other grasses and grass-like plants (Table 3.1, Figure 3.4). This suggests that the initial rate of growth for the other grasses and grass-likes plants was initially slower than the initial rate of growth for *Festuca hallii*, which had a quadratic regression. A lower growth rate

Table 3.1 Coefficients of determination for sward dry matter yield (SWYL), *Festuca hallii* (*Fh*) dry matter yield (FHYL), other grasses and grass-like plants dry matter yield (OGYL), forbs and woody dry matter yield (FWYL), *Fh* sward composition (FHSW%), other grasses and grass-like plants (OGSW%), forbs and woody species (FWSW%), *Fh* extended leaf height (ELH), *Fh* green leaf height (GLH), *Fh* crude protein (CP%), *Fh* crude protein yield (CPYL), *Fh* neutral detergent fibre (NDF%), *Fh* acid detergent fibre (ADF%), *Fh* hemicellulose (HC%), *Fh* cellulose (CL%), *Fh* acid detergent lignin (ADL%), *Fh* stem base weight (SBWT), *Fh* stem base total nonstructural carbohydrate percentage (SBTNC%), *Fh* stem base total nonstructural carbohydrate pool (SBTNCPL) and *Fh* root weight (RTWT) as a function of Julian date in 1987 using linear, quadratic, cubic, quartic and quintic regressions.

	Polynomial Regression				
Parameter	Linear	Quadratic	Cubic	Quartic	Quintic
SWYL	.38 b ***	**.68** a ***	.68 a ***	.69 a ***	.70 a ***
FHYL	.33 b ***	**.57** a ***	.57 a ***	.57 a ***	.58 a ***
OGYL	.13 c ***	.22 b ***	**.26** a ***	.26 a ***	.26 a ***
FWYL	.09 b **	**.18** a ***	.18 a ***	.18 a ***	.19 a **
FHSW%	.01 a	.03 a	.03 a	.03 a	.03 a
OGSW%	.01 b	.01 b	.06 a	.06 a	.06 a
FWSW%	.00 a	.02 a	.03 a	.03 a	.03 a
ELH	.21 d **	.76 c ***	.86 b ***	**.89** a ***	.89 a ***
GLH	.00 d	.76 c ***	.83 b ***	**.89** a ***	.89 a **
CP%	.73 c ***	.89 b ***	**.99** a ***	.99 a ***	.99 a ***
CPYL	.14 c ***	.48 b ***	.49 b ***	**.55** a ***	.56 a ***
NDF%	.80 c ***	**.92** b ***	.92 b ***	.93 b ***	.95 a ***
ADF%	.76 c ***	.86 b ***	**.90** a ***	.91 a ***	.91 a ***
ADL%	**.81** a ***	.81 a ***	.83 a ***	.83 a ***	.83 a ***
CL%	.66 c ***	.81 b ***	**.87** a ***	.87 a ***	.87 a ***
HC%	**.39** b **	.47 b **	.54 b *	.63 b **	.77 a **
SBWT	.00 b	.06 a *	.08 a *	.08 a	.09 a
SBTNC%	.06 d ***	.34 c ***	.34 c ***	.55 b ***	**.63** a ***
SBTNCPL	.01 b	.02 b	.03 b	.06 b	.10 b
RTWT	.04 a	.04 a	.06 a	.07 a	.07 a

Bold numbers indicate r^2/R^2 for polynomial used in results and discussion.
Similar letters of coefficients of determination for a parameter indicate no significant difference in reduction of regression sums due to fitting a higher-degree polynomial.
*, **, *** indicate significant regressions for $P<0.05$, 0.01 and 0.001, respectively.

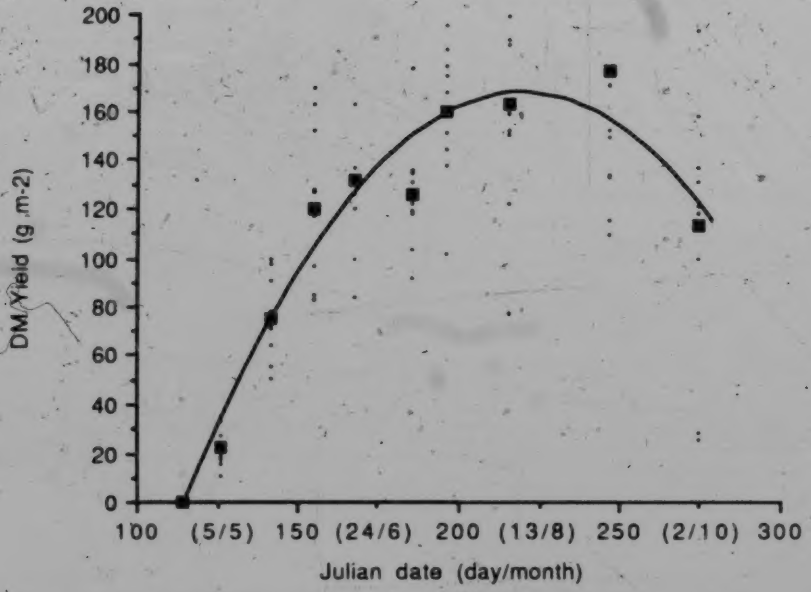

Figure 3.2 Dry matter (DM) yield of a *Festuca-Stipa* sward through the 1987 growing season as a function of Julian date. Boxes indicate sampling date mean (n=10).

$y=-568.88+6.6914x-0.01520x^2$, $R^2=0.68$.

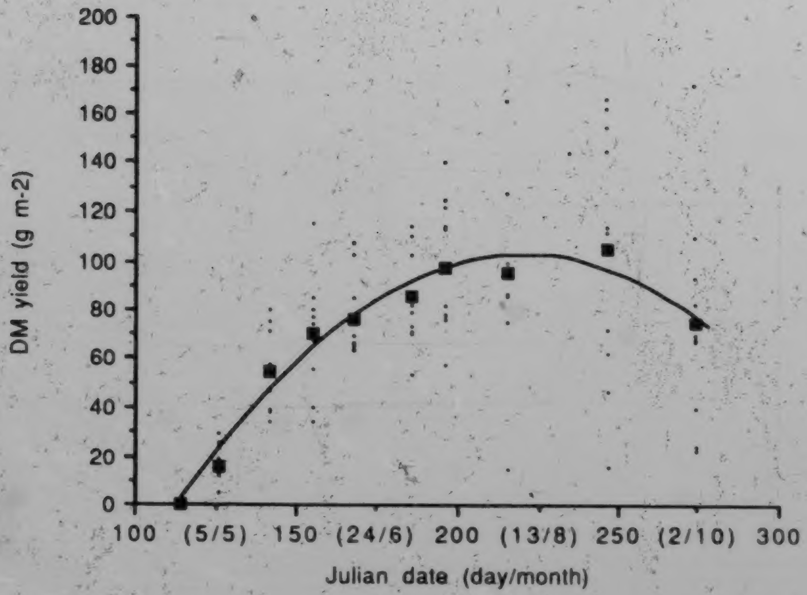

Figure 3.3 Dry matter (DM) yield of *Festuca hallii* through the 1987 growing season as a function of Julian date. Boxes indicate sampling date mean (n=10).

$y=-330.42+3.9133x-0.0088x^2$ $R^2=0.57$.

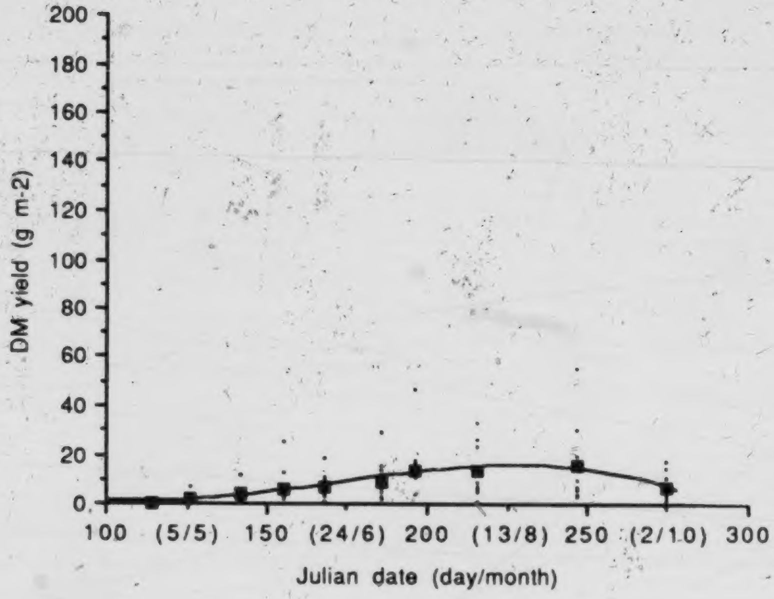

Figure 3.4 Dry matter (DM) yield of the other grasses and grass-like species through the 1987 growing season as a function of Julian date. Boxes indicate sampling date mean (n=10). $y=67.397-1.4181x+0.00940x^2-0.00002x^3$. $R^2=0.26$.

during May for the other grasses and grass-like plants compared to *Festuca hallii* would be consistent with work done on comparative crop growth rates by Willoughby et al. (in prep.). The cubic regression suggests that the aboveground DMY for the other grasses and grass-like plants would peak about August 17th (229).

Curve fitting using stepwise polynomial regressions yielded a quadratic regression ($P<0.001$, $R^2=0.18$) for the aboveground DMY for the forbs and woody species. This regression suggested that optimum spring growth occurred from April 24th (114) to June 17th (168) and aboveground DMY peaked about August 6th (216) (Figure 3.5).

Senescence was more rapid for the forbs and woody species than for *Festuca hallii* and the other grasses and grass-like plants from September 4th (247) to October 2nd (275) (Figure 3.1).

Sward Composition

The average sward composition (DM%) during the growing season was 65% for *Festuca hallii*, 8% for the other grasses and grass-like plants, and 27% for the forbs and woody species. Curve fitting using stepwise polynomial regressions yielded no significant regression relationships for sward composition as a function of Julian date for the aboveground sward components (Table 3.1).

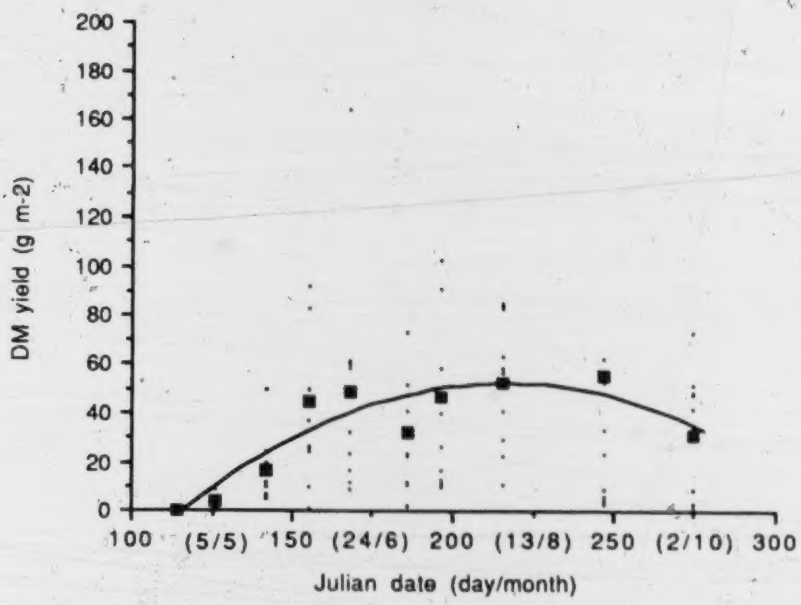

Figure 3.5 Dry matter (DM) yield of the forbs and woody species through the 1987 growing season as a function of Julian date. Boxes indicate sampling date mean (n=10).

$y=-190.93+2.2385x-0.00515x^2 \quad R^2=0.18.$

After June 4th (155) the sward composition of the forbs and woody species declined, reflecting their decreased growth rate which was likely associated with the low amount of precipitation during June (Figures 3.1, 3.6). The sward composition of the grasses increased slightly during this same period. From July 3rd (184) to August 4th (216) the forbs again increased in sward composition while the grasses declined, likely reflecting the improved moisture conditions during July. From August 4th (216) to October 2nd (275) *Festuca hallii* increased in sward composition which was probably related to the decline in the forbs and woody species sward composition from August 4th (216) to September 4th (247) which was then followed by a decline in the sward composition of the other grasses and grass-like plants from September 4th (247) to October 2nd (275).

Leaf Height and Senescence

The extended leaf height of *Festuca hallii* was measured on the sampling dates through the growing season. The height of the photosynthetically active green portion of the leaves was also measured. This provided a measure of the photosynthetically active versus senesced portions of the *Festuca hallii* leaves as the growing season progressed.

Senescence in *Festuca hallii* was characterized by initial browning at the leaf tip. The brown continued toward the base of individual leaves as the growing season progressed. The rate of

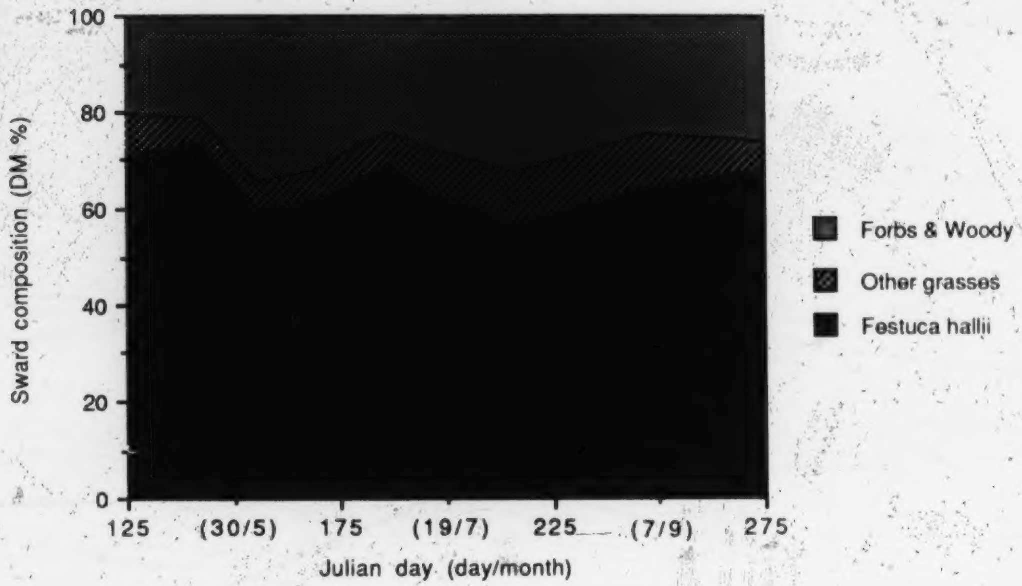

Figure 3.6 Sward composition of *Festuca hallii*, other grasses and grass-like species, and forbs and woody species through the 1987 growing season by sampling date.

senescence for an individual leaf would appear to be a function of tiller age. Young leaves that were green to their tips were observed in August and early September while older leaves had senesced almost completely. The tightly folded morphology of the leaves did not appear to change with time or other environmental factors.

Curve fitting using stepwise polynomial regressions yielded quartic regressions for both the extended leaf height ($P<0.001$, $R^2=0.89$) and the green leaf height ($P<0.001$, $R^2=0.89$) of *Festuca hallii* (Table 3.1, Figure 3.7).

Extended leaf height increased rapidly from April 24th (111), with the fitted curve suggesting a peak about June 24th (175) at an extended height of approximately 22 cm (Figure 3.7). Actual extended leaf height peaked on August 4th (216) and then began to decline as the growing season progressed through August and September. The sampling technique was biased to measuring the longest leaves and therefore leaves from the sward's older tillers. The decline in leaf height may reflect the point when the water content of the plant begins to decline.

The extended green leaf height for *Festuca hallii* in the sward peaked on June 4th (155) for the actual data, but the fitted curve suggested a peak about June 11th (162) (Figure 3.7). After June 4th (155) there was a moderate but steady decline in the height of the green photosynthetically active tissue until August 4th (216). After August 4th (216) there was a more rapid rate of decline for

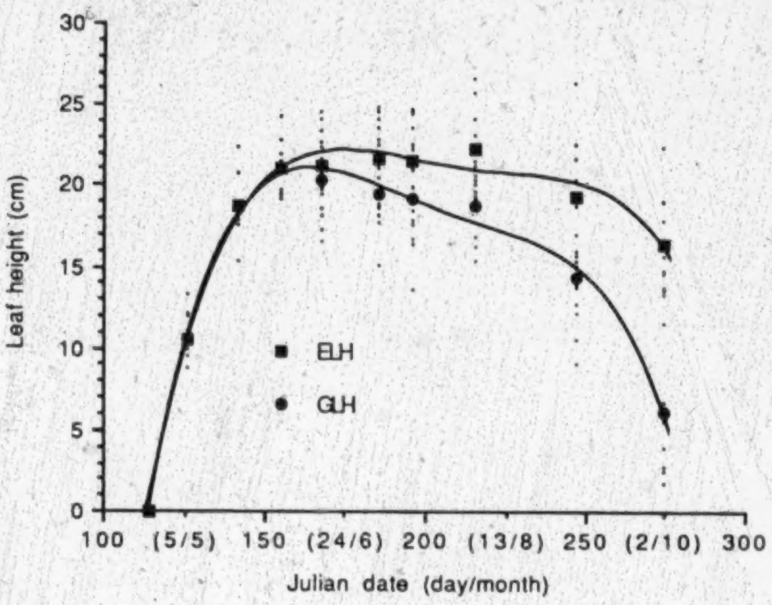

Figure 3.7 Extended leaf height (ELH) and green leaf height (GLH) of *Festuca hallii* through the 1987 growing season as a function of Julian date (n=10).

$ELH=-598.616+11.39981x-0.0816778x^2+0.0002579x^3-0.0000003x^4 \quad R^2=0.89$

$GLH=-689.162+14.023619x-0.105238x^2+0.0003432x^3-0.0000004x^4 \quad R^2=0.89$

the height of green tissue in the leaves. The regression for the green leaf height suggests that this decline accelerated sharply after September 4th (247).

Growth Stage

Phenology of *Festuca hallii* was noted on each sampling date using the growth stage terminology of Metcalfe (1973) (Table 3.2). The progression from vegetative to anthesis growth stage occurred during the first six weeks of the growing season, from late April to early June in 1987. Ripe seed of *Festuca hallii* was observed by the beginning of July with heads beginning to shatter by early August. *Festuca hallii* was beginning to cure and enter a winter dormancy state by early October.

Forage Quality

Curve fitting using stepwise polynomial regressions yielded a cubic regression ($P<0.001$, $R^2=0.99$) for CP (%) and a quartic regression ($P<0.001$, $R^2=0.55$) for the CP yield (Table 3.2, Figure 3.8). Crude protein percentage (CP (%)) decreased rapidly through May from a high of 16.9%. The CP (%) decline began to level off at the 10% level which coincided with the cessation of leaf extension during the middle of June (Figures 3.7). The CP (%) decline then progressed more slowly through the remainder of June before stabilizing between 9.1% and 8.5% from the beginning of July to the beginning of September during the ripe seed and postripe growth stages. There was a decline to 6.5% on October 2nd (275).

Table 3.2 Growth stage; foliage: crude protein percentage (CP), crude protein yield (CPYL), neutral detergent fibre percentage (NDF), acid detergent fibre percentage (ADF), acid detergent lignin percentage (ADL), cellulose percentage (CL), hemicellulose percentage (HC); and stem base total nonstructural carbohydrates percentage (TNC) for *Festuca hallii* by sampling date in 1987.

Day/Month	6/5	22/5	4/6	17/6	5/7	15/7	4/8	4/9	2/10
Julian Date	126	142	155	168	186	196	216	247	275
Growth Stage	Boot	Heading	Anthesis	Milk	Ripe Seed	Ripe Seed	Postripe	Postripe	Stem-cured
CP (%)	16.9	13.4	11.3	10.0	9.1	8.5	8.7	8.8	6.5
CPYL (g m^{-2})	2.7	7.4	7.9	7.6	7.8	8.4	8.3	9.3	4.9
NDF (%)	56.5	56.2	62.0	63.8	64.6	65.3	66.4	67.8	68.3
ADF (%)	32.0	34.1	37.8	39.6	39.0	38.9	41.2	41.4	42.8
ADL (%)	1.8	1.9	1.8	2.4	2.2	2.3	3.0	3.2	3.4
CL (%)	30.2	32.2	36.1	37.2	36.8	36.6	38.2	38.2	39.4
HC (%)	24.4	22.1	24.2	24.2	25.6	26.4	25.2	26.3	25.5
TNC (%)	11.2	11.2	10.9	11.6	12.0	10.6	10.0	10.3	12.8

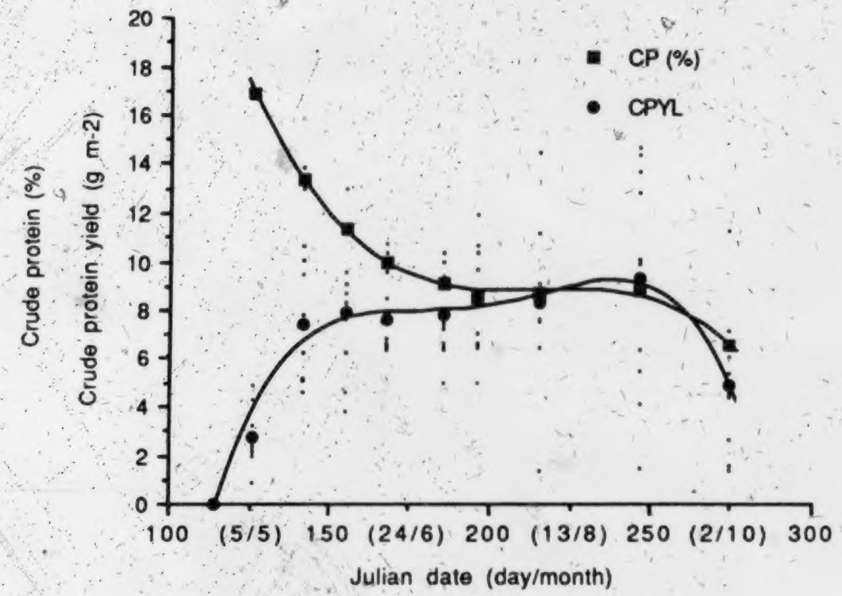

Figure 3.8 Crude protein percentage (CP (%)) and crude protein yield (CPYL) of *Festuca hallii* through the 1987 growing season as a function of Julian date (CP, n=2; CPYL, n=10).

$\text{CP}\ (\%)=126.16-1.6362x-0.00759x^2+0.00002x^3 \quad R^2=0.99$

$\text{CPYL}=-317.161+6.7544x-0.052267x^2+0.000178x^3-0.0000002x^4 \quad R^2=0.55$

Festuca hallii DMY continued to increase until September 4th (247) which when multiplied by the CP (%) resulted in a CP DMY that peaked in September (Figure 3.8). There was no major increase in the CP DMY after the May 22nd (142) sampling date.

Curve fitting using stepwise polynomial regressions yielded a quadratic regression ($P<0.001$, $R^2=0.92$) for the neutral detergent fibre percentage (NDF (%)) (Tables 3.1, 3.2, Figure 3.9). The quadratic regression for the NDF (%) as a function of Julian date showed a rapid increase from early May with a leveling off about the end of July. A slight decline in NDF (%) was indicated by the regression after the beginning of September. This probably indicates that the regression underestimated the actual NDF (%) as the plant approached winter dormancy. The NDF content leveled off as *Festuca hallii* entered the dormant season. This was associated with the low rate of increase in the acid detergent lignin percentage (ADL (%)) (Figure 3.10), combined with the small changes in hemicellulose percentage and cellulose percentage for the August to September period.

For the acid detergent fibre (ADF (%)), curve fitting using stepwise polynomial regressions yielded a cubic regression ($P<0.001$, $R^2=0.90$) suggesting three time phases (Tables 3.1, 3.2, Figure 3.9). ADF (%) increased rapidly from May 6th (126) to June 17th (168) after which it leveled off until after July 15th (196) when it began to increase again. These three phases correspond to the rapid growth from the boot to milk growth stages, then the ripe

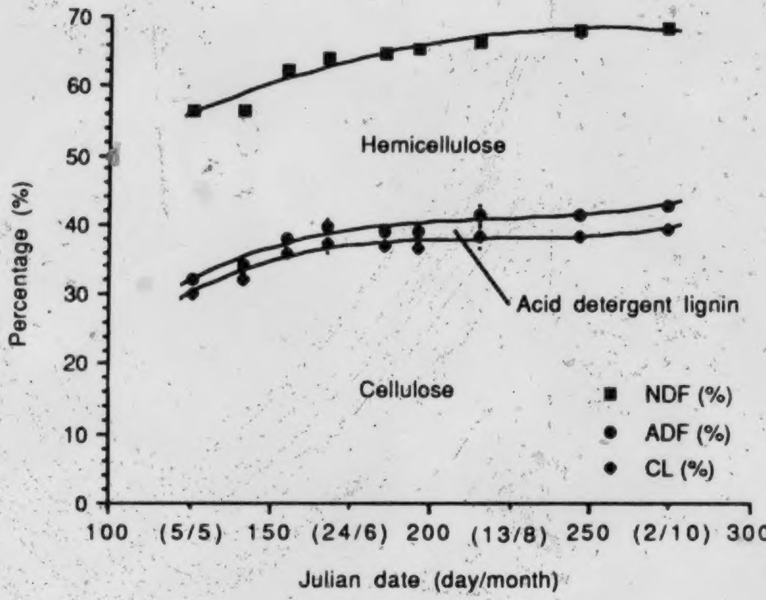

Figure 3.9 Neutral detergent fibre percentage (NDF (%)), acid detergent fibre percentage (ADF (%)), and cellulose percentage (CL (%)) of *Festuca hallii* through the 1987 growing season as a function of Julian date (n=2). Hemicellulose = NDF (%) - ADF (%). Acid detergent lignin = ADF (%) - CL (%).

NDF $(\%)=21.0945+0.365768x-0.00071x^2$ $R^2=0.92$

ADF $(\%)=-51.8877+1.22668x-0.00549x^2+0.000008x^3$ $R^2=0.90$

CL $(\%)=-59.3489+1.321845x-0.006013x^2+0.000009x^3$ $R^2=0.87$

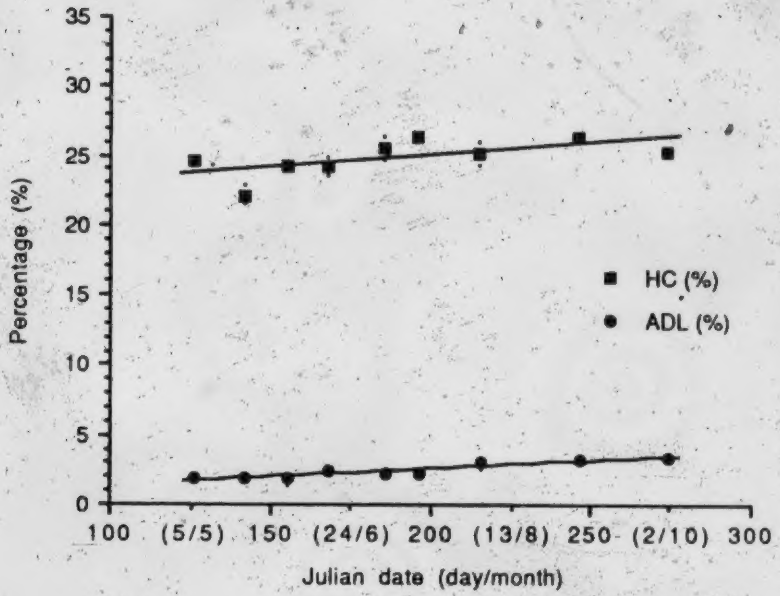

Figure 3.10 Hemicellulose percentage (HC (%)) and acid detergent lignin percentage (ADL (%)) of *Festuca hallii* through the 1987 growing season as a function of Julian date (n=2).

HC (%)=21.4287+0.01825x R^2=0.39

ADL (%)=0.22685+0.01166x R^2=0.81

seed growth stage, and finally the postripe and stem-cured growth stages as the plant began to mature prior to winter dormancy (Table 3.2)

Curve fitting using stepwise polynomial regressions yielded a linear regression ($P<0.001$, $r^2=0.81$) for the acid detergent lignin percentage (ADL (%)) (Table 3.2, Figure 3.10). ADL (%) increased gradually from 1.8% on May 5th (126) to 3.4 % on October 2nd (275).

The use of nuclear magnetic resonance (NMR) spectroscopy (Efloson et al. 1984) for *Festuca hallii* indicated that by the end of the growing season there was a lower degree of ether cross linkage within the cellulose-lignin complex than in timothy (Cyr et al. 1988). This suggested that at the end of the growing season the cellulose-lignin complex of *Festuca hallii* may be qualitatively different from those of other perennial forage grasses such as timothy, thereby increasing the relative autumn digestibility of *Festuca hallii* during the postripe, stem-cured and weathered growth stages.

Curve fitting using stepwise polynomial regressions yielded a cubic regression ($P<0.001$, $R^2=0.87$) for the cellulose percentage (CL (%)), suggesting three phases similar to those identified for the ADF (%) (Tables 3.1, 3.2, Figure 3.9). This would be expected as the cellulose content is calculated by subtracting the ADL (%) from the ADF (%).

Curve fitting using stepwise polynomial regressions yielded a linear regression ($P<0.01$, $r^2=0.39$) for the hemicellulose percentage (HC (%)) (Table 3.2, Figure 3.10).

Stem base weight, TNC (%), and TNC pool.

The *Festuca hallii* stem base weights ranged between 399 and 646 g m^{-2} among sampling date means with an overall average of 490 g m^{-2}. The stem base TNC pool ranged between 45.0 and 75.4 g m^{-2} among sampling date means with an overall average of 55.9 g m^{-2}. The sampling date means for TNC (%) are listed in Table 3.2 with the exception of the April 24th (114) sampling date which was 14.8%.

Curve fitting using stepwise polynomial regressions yielded a quadratic regression ($P<0.05$, $R^2=0.06$) for stem base weight and a quintic regression ($P<0.001$, $R^2=0.63$) for TNC (%) but no significant regression ($P>0.05$) for stem base TNC pool, with each regression calculated as a function of Julian date (Table 3.1, Figure 3.11). As the quadratic regression for the stem base weight had a coefficient of determination of only 6%, it was not used.

The pattern of the quintic regression for TNC (%) as a function of Julian date is initially consistent with the transition of a plant changing rapidly from a winter dormancy stage through a vegetative state to a boot growth stage in a period of two weeks with the April 24th (114) TNC value of 14.8 % declining to 11.2% on May 6th (126) (Table 3.2, Figure 3.11). The TNC (%) remained low through

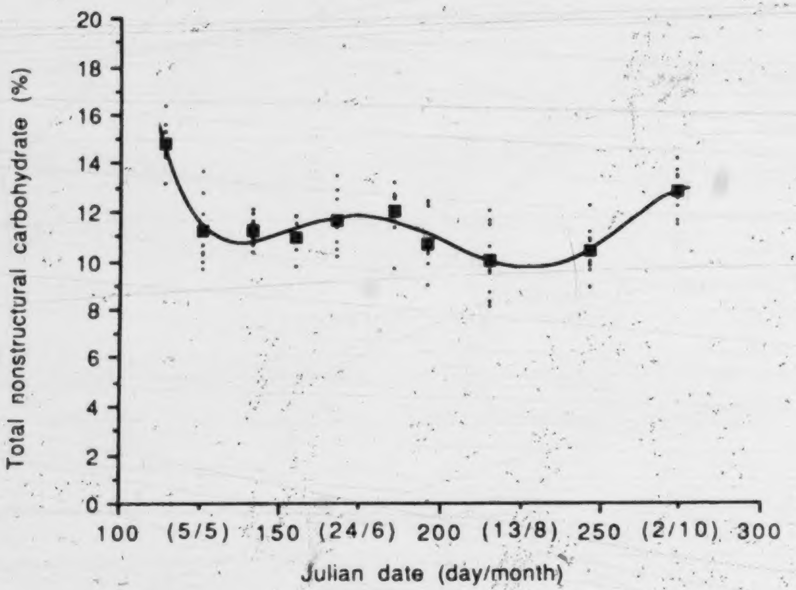

Figure 3.11 Stem base total nonstructural carbohydrate percentage (TNC (%)) of *Festuca hallii* through the 1987 growing season. Circles indicate sampling date mean as a function of Julian date (n=10).

TNC $(\%)=924.15-24.4596x+0.256020x^2-0.001308x^3$
$+0.000003x^4-0.000000003x^5$ $R^2=0.63$

the heading and anthesis growth stages before increasing slightly to 11.6 and 12.0 TNC (%) during the milk and early seed ripe growth stages. As the plant moves through the ripe seed and postripe growth stages the TNC (%) decreases again to a low of 10.0%. Only when the plant went from the postripe to the stem-cured growth stage in September did the TNC (%) increase again to 12.8%.

Root Weights

The *Festuca hallii* root DM weights to the 7.5 cm depth ranged between 642 and 885 g m^{-2} among sampling date means with an overall average of 750 g m^{-2}. Curve fitting using stepwise polynomial regressions yielded no regression ($P>0.05$) for root DM weights to the 7.5 cm depth as a function of Julian date (Table 3.1).

DISCUSSION

Sward Dynamics

The aboveground DMY for the sward as a whole, for *Festuca hallii*, and the forb and woody components followed a quadratic function with time through the 1987 growing season. In contrast, the aboveground DMY for the other grasses and grass-like plants was a cubic function of time in the growing season. The cubic regression for the other grasses and grass-like species suggested a delayed start for optimum spring growth until late June and July at which time *Festuca hallii* growth had slowed compared with its growth rate in May (Figures 3.1, 3.3, 3.4).

A distinction between the optimum growth periods for *Festuca hallii* compared to the other grasses and grass-like plants has important implications for sward composition in terms of the effects of the timing of the first spring defoliation. Defoliation between early May and early June would remove foliage of *Festuca hallii* at the time of optimum growth. *Festuca hallii* regrowth would then be stimulated at a time when its optimum growth period was ending. In contrast, the optimum growth period for the other grasses and grass-like plants was from early June to early July. Competitive growth between early June and early July would therefore likely favor the other grasses and grass-like plants over growth of *Festuca hallii*. Delaying the first sward defoliation until after the beginning of July would likely reduce this advantage for the other grasses and grass-like species because at that time their growth rate would also be declining. A deferred-rotation grazing management system in contrast to the traditional heavy continuous grazing management system could likely capitalize on these sward component growth differences to maintain the vigor and sward composition of *Festuca hallii*.

There were no significant regressions to describe the growing season changes in sward composition as a function of time (Table 3.4, Figure 3.6). This indicated that in the absence of defoliation, the sward composition of *Festuca hallii*, other grasses and grass-like plants, and forbs and woody species remained relatively constant throughout the growing season. This comparative constancy was independent of the differences in optimum growth periods for *Festuca hallii* compared to the other grasses and grass-like plants. This stability in sward composition through the growing season was probably associated with the two major components: *Festuca hallii* at 65%, and the forbs and woody species at 27%, both having the same quadratic growth pattern and together making up 92% of the sward composition. The cubic growth pattern of the other grasses and grass-like plants did not affect the sward composition through the growing season and this was likely associated with the other grasses and grass-like plants making up only 8% of the sward composition. This study needs to be repeated over a number of consecutive years to confirm whether the *Festuca-Stipa* sward composition values reported for 1987 reflect those of a successionally stable community.

It is likely, however, that repeated years of defoliation initiated between early May and early June would increase the sward composition of the other grasses and grass-like species by giving them a competitive advantage over the grazed *Festuca hallii*. This would probably be associated with the differences between the optimum May growth period for *Festuca hallii* versus the optimum June growth period for the other grasses and grass-like plants (Willoughby et al. in prep.).

Festuca hallii Dynamics

Leaf height of *Festuca hallii* increased rapidly from the end of April until early June (Figure 3.7). By the middle of June extended leaf length had reached a plateau. This is consistent with the three-year study in south-central British Columbia reported by Stout et al. (1981) for *Festuca campestris*. Senescence, as measured by leaf tip browning, was apparent at the beginning of June which indicated that early June was a point of change in terms of leaf growth. This abrupt cessation in leaf extension coincided with the plant entering the milk growth stage (Table 3.2). Senescence progressed as a linear function of Julian date from early June to early September and then accelerated rapidly. This change in senescence rate coincided with a change in a number of forage quality factors associated with the plant entering the stem-cured growth stage prior to winter dormancy. Extended leaf height also declined after August 4th (216), possibly reflecting a point at which water content began to decline in older leaves. This coincided with the plant entering the postripe growth stage.

Given that May and June had only 74 % and 62 % of the accumulated long term average precipitation, this study needs to be repeated over several years to determine whether more normal precipitation patterns would result in higher extended leaf heights, extended leaf heights peaking later in the growing season, and a slower and more delayed rate of senescence.

The phenology of *Festuca hallii* at this study site was characterized by very rapid movement from vegetative to anthesis growth stages in a period of six weeks from late April to early June (Table 3.2). If the retention of *Festuca hallii* in the sward is a management objective, then defoliation during this period of very vigorous growth and rapid physiological change should be avoided.

The crude protein percentage (CP (%)) values in this study are 2 to 3% higher than those reported by Johnston and Bezeau (1962) for what was probably *Festuca campestris* from southwestern Alberta and those by Pidgen (1953) for what was probably *Festuca hallii* from southwestern Saskatchewan. The CP content of 6.5% in October, however, is consistent with the weathered (March) CP content of 5.0% for what was probably *Festuca hallii* in west-central Montana (Dragt and Havstad 1987). The differences between the CP (%) values for *Festuca hallii* in this study and those in the studies of 1953 and 1962 suggest a need for a new comprehensive study to compare the forage quality parameters of *Festuca hallii* with other important forage species in Western Canada.

The rapid decrease of crude protein percentage (CP (%)) through May was probably associated with the rapid growth in leaf height and the associated increase in the cell wall content of the leaves (Figures 3.7, 3.8, 3.9). The leveling off of the CP (%) that coincided with the plateauing of extended leaf height at about 22 cm in mid-June would be consistent with cessation of leaf extension for a plant about to enter the ripe seed growth stage

(Table 3.2). In September there appeared to be an association between protein decline and the rapid development of leaf senescence. This was probably associated with the process of winter hardening as the plant entered the stem-cured growth stage and prepared for winter dormancy.

Of particular note was how CP (%) remained greater than 8.5% until early September when the yield of CP (g m^{-2}) reached a peak (Figure 3.8). It is also important to note that CP yield did not exhibit a major increase after the May 22nd (142) sampling date. Traditional continuous grazing practices in east central Alberta have cattle going onto *Festuca-Stipa* grasslands as early as the end of April or early May. Early May would coincide with the CP (%) of *Festuca hallii* approaching its maximum value. This is also the time, however, when the plant would be physiologically vulnerable given the growth processes associated with the rapid increase in extended leaf height and growth stage changes during May (Figure 3.7, Table 3.2). The results of this study suggest that delaying grazing until as late as early September when *Festuca hallii* would be more physiologically robust, would enhance rather than compromise the grassland's CP yield compared to early June. The practicality of implementing this type of delay would depend upon the development of a deferred-rotation grazing system for a *Festuca-Stipa* grassland, or the development of a complementary grazing system if other forage sources were available.

If the pattern for CP yield described above was found to be repeated over a number of years, this would demonstrate an important advantage of *Festuca hallii* over other species for the purpose of late summer grazing, and confirm a significant role for late summer *Festuca-Stipa* grassland use in complementary grazing systems in the Aspen parkland. It would also suggest that nutritionally this plant is well suited for deferred-rotation grazing systems.

The rapid NDF (%) increase from mid-May to mid-June suggested a window of defoliation vulnerability during which the plant could be more sensitive in terms of season of defoliation (Table 3.2, Figure 3.9). This is the same period associated with the maximum increase in extended leaf height and the most rapid changes for growth stage. NDF% has been inversely correlated with the voluntary dry matter intake (DMI) of forages (Rohweder et al. 1978). This suggests that DMI for *Festuca hallii* would likely remain fairly constant from mid-July till mid-autumn as there was little increase in NDF% after the middle of July.

Acid detergent fibre content (ADF (%)) has been shown to be inversely correlated with *in vivo* digestibility or digestible dry matter (DDM) for a number of temperate and subtropical forages (Rohweder et al. 1978). The ADF (%) values reported for *Festuca hallii* in this study are in the low end of the range of ADF (%) values reported for *Bromus inermis*, *Dactylis glomerata*, *Phalaris arundinacea* and *Festuca arundinacea* by Rohweder et al. (1978).

This would suggest that the DDM, or *in vivo* digestibility, of *Festuca hallii* would be equal, or superior, to that of these other species.

The acid detergent lignin content (ADL (%)) of 1.8 to 3.4% in this study was in the same range as the 2.6 to 3.9% reported by Dragt and Havstad (1987) for what was likely *Festuca campestris* (weathered) from west-central Montana, but lower by 2 to 3% compared to the 4.5 to 6.2% reported by Pidgen for what was probably *Festuca campestris* from south-western Saskatchewan by Pidgen (1953) (Table 3.2). The Dragt and Havstad (1987) and Pidgen (1953) studies both indicated that the *Festuca campestris* ADL (%) was consistently lower than that for the other grass species they studied. This was particularly evident at the "mature" or "cured" growth stage.

A linear relationship with only a slight increase in acid detergent lignin (ADL (%)) with Julian day for *Festuca hallii* during the growing season was indicated in this study (Tables 3.1, 3.2, Figure 3.10). This is important as the digestibility of the cellulose and hemicellulose components of the cell wall are a function of the degree of their lignification (Pearson and Ison 1987). The comparatively low ADL (%) at the end of the growing season combined with a low degree of ether cross linkages within the cellulose-lignin complex in *Festuca hallii* would likely enhance the late summer or early autumn digestibility of this species in comparison to other species with higher ADL (%) values and higher degrees of ether cross linkages. This forage quality aspect of

Festuca hallii could be of particular value if grazing was timed to coincide with the peak of CP yield in the late summer.

Cellulose percentage (CL (%)) and acid detergent fibre percentage (ADF (%)) both had similar cubic regressions as functions of Julian date (Tables 3.1, 3.2, Figure 3.9). This similarity would be related to the CL (%) being calculated by subtracting the ADL (%) from the ADF (%). The CL (%) values followed the ADF (%) values with a gradually increasing separation reflecting the effect of the slight linear increase in the ADL (%) as the growing season progressed. The cubic function suggests a slight increase in the cellulose content at the end of growing season which would be consistent with the plant entering the stem-cured growth stage.

Hemicellulose content (HC (%)), in contrast to the other fibre components, increased through the growing season as a linear function of time, and at a rate of increase slightly higher than that for ADL (%) (Table 3.1, Figure 3.10). The hemicellulose values of 22.1 to 26.4% reported in this study fall within the range of 22.5 to 28.3% reported by Moore and Mott (1973) as typical for temperate species (Table 3.2). A slight increase in cellulose buildup over hemicellulose buildup as the plant entered the stem-cured growth stage was suggested with the plateauing of the NDF content (quadratic regression) and the increase in ADF content (cubic regression) at the end of the growing season (Figure 3.9). The repeatability of this suggested trend needs to be established with further experimentation and sampling through several winters to monitor how these forage quality factors change as *Festuca hallii* weathers.

The *Festuca hallii* forage quality attributes discussed above, especially as expressed by the CP yield and ADL (%) characteristics, help to explain why this species has enjoyed a reputation for good late summer and autumn grazing. Further work needs to be done to explore the relationships between the parameters described in this study and the digestibility characteristics of *Festuca hallii*.

Neither stem base weights nor total nonstructural carbohydrate (TNC) pool changed significantly during the growing season. This suggested that these parameters remained stable under no defoliation stress throughout the growing season regardless of the plant's growth process or stage. If this characteristic was verified, then it could provide the basis for a control with which the stress of defoliation experiments might be assessed by changes in stem base weights and stem base TNC pools.

Stem base TNC (%) did change significantly as a function of Julian date (Table 3.1 Figure 3.11). These results suggested that *Festuca hallii* may be characterized more by a flat or extended than a narrow V shaped TNC cycle. The flat or extended TNC cycle has been associated with species more susceptible to defoliation stress (Menke and Trlica 1981). The increase in stem base TNC (%) in late June and early July during 1987 may not be typical, but possibly an osmoticant effect associated with the water stress of

June 1987. The lowest stem base TNC (%) values between early August and early September may be associated with late summer foliage and root growth which is characteristic of cool season grasses. The comparatively high October 2nd (275) TNC value of 12.8% likely reflects the plant preparing for winter dormancy with the initiation of winter hardening.

If the quintic function in which there is an initial dip in the TNC (%) in late May before the peak in late June and early July was shown to be typical, defoliating the plant in late May and early June, as is commonly done, would catch it at a point in which the TNC (%) was at its second lowest point in the growth cycle which could contribute to its physiological vulnerability at that point in the growing season (Figure 3.11). In contrast, the highest stem base TNC (%) levels were in late-April, late June to early July, and late September to early October. Defoliation at these times in the growth cycle may have minimal defoliation stress effects given the comparatively high TNC (%) levels.

Root DM weights to a depth of 7.5 cm did not change significantly during the growing season. This suggested that root weights to the 7.5 cm depth remained stable under no defoliation stress through the growing season, regardless of the plant's growth process or growth stage. As for stem base weight and stem base TNC pool, if this characteristic was verified for root weight to the 7.5 cm depth, then it could provide the basis for a control with which to measure the stress of defoliation treatments on *Festuca hallii*.

The logical period for the greatest physiological vulnerability to defoliation stress for *Festuca hallii* would fall between the end of April and the beginning of June for the following reasons. Almost all the increase in extended leaf height was completed between the end of April and the middle of June at which time the beginning of leaf senescence started with leaf tip browning. During the same period the plant moved rapidly through the vegetative, boot, heading and anthesis growth stages with ripe seed developing by early July. This period of vulnerability would appear to coincide with an initial TNC (%) depression between the middle of May and the middle of June. This interval also coincides with the period of maximum NDF (%) increase, again reflecting the rapid growth changes that occurred within the plant from the end of April to the beginning of May.

CONCLUSIONS

There was no major shift in the relative sward composition of *Festuca hallii* (65%), other grasses and grass-like plants (8%), and forb and woody species (27%) components during the 1987 growing season. The *Festuca hallii* sward component, and the forb and woody species component, were both characterized by quadratic growth cycles whereas the other grasses and grass-like plant sward component had a cubic growth cycle with a slower start for spring growth. The differences between the growth cycles of *Festuca hallii* and the other grasses and grass-like sward components did not affect the sward composition through the growing season. These same differences, however, have important implications for the effect of the timing of the first defoliation on the relative competitiveness of *Festuca hallii* in relation to the competitiveness of the other grasses and grass-like plants.

Crude protein percentage for *Festuca hallii* was greater than 8.5% throughout the growing season, which when combined with its DMY gave the greatest CP yield between August and September. *Festuca hallii* 's reputation as an excellent autumn forage is likely based on this pattern of CP yield, combined with its low lignin (%) and low degree of ether cross-linkage in the cellulose-lignin complex.

Festuca hallii is not physiologically adapted to defoliation in the spring, especially during the period from early May to late June. The growth and forage quality characteristics indicate that it is well suited to summer (early July) and autumn (September to October) defoliation. The basic growth and forage quality cycles of *Festuca hallii* therefore suggest that this species is biologically suited for utilization in complementary or deferred-rotation grazing systems in central Alberta.

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IV. EFFECTS OF SEASON OF DEFOLIATION ON PLAINS ROUGH FESCUE IN CENTRAL ALBERTA

INTRODUCTION

The biological responses of a forage plant to defoliation are partially a function of the season, or the time of year, when defoliation occurred. Major grass species within the same grassland can have different regrowth responses to the same season of defoliation event (Bailey and Anderson 1978). The start of the growing season is a critical growth period for many forage species and therefore care is required in terms of when grazing is initiated (Stoddart et al. 1975). In terms of date of range readiness for grazing, differences between the phenological growth stages of a grassland's important species (Costello and Price 1939) and their physiological flexibility in response to defoliation (Caldwell et al. 1981) may lead to shifts in sward composition and range condition as a function of season of defoliation management practices. The development of grazing system recommendations which will facilitate the maintenance or improvement of range condition for a given grassland are dependent on an understanding of how season of defoliation affects the vigor of the key species, and the species composition of that grassland.

Central Alberta livestock operations almost always involve winter feeding of preserved forages. Therefore, there is economic pressure to use grazing lands, including native *Festuca-Stipa* grasslands, as early in the spring and as late in the autumn as possible. The pervasive practice of heavy continuous grazing in central Alberta has been shown to create a negative range trend for *Festuca-Stipa* grasslands (Bailey et al. 1988).

Festuca hallii (Vasey) Piper [1] is the key species in the *Festuca-Stipa* grasslands of central Alberta (Pavlick and Looman 1984, Wroe et al. 1988). This native grassland has been shown to have forage production equal to, or better than, the forage production of introduced *Bromus inermis-Festuca rubra* grasslands in the absence of a legume (Bailey et al. 1980). Average daily gains for steers of 1.1 kg under light (8 AUM) June grazing and 0.8 kg under light (8 AUM) autumn grazing on *Festuca-Stipa* grassland has been shown over a 11-year grazing study by Bailey et al. (1988). Most of this weight gain performance was attributable to *Festuca hallii* which may contribute more than 70% of the forage dry matter yield from *Festuca-Stipa* grasslands of central Alberta.

There has been some confusion in both the taxonomy and nomenclature of the North American rough fescues (Pavlick and Looman 1984; Harms 1985). Historically, the key species in the *Festuca-Stipa* grasslands of the aspen parkland of central Alberta and the *Festuca-Danthonia* grasslands of the Rocky Mountain foothills of south-western Alberta, has been called *Festuca scabrella* (Moss 1983). The rough fescues of these two regions have been commonly distinguished as the plains rough fescue and foothills rough fescue, respectively. The species nomenclature for the North American rough fescues as proposed by Pavlick and Looman (1984) will be followed in this paper with the plains rough fescue identified as *Festuca hallii* (Vasey) Piper and the foothills rough fescue as *Festuca campestris* Rydb.. When literature cited refers to *Festuca scabrella*, an effort will be made to interpret that literature as *Festuca campestris* or *Festuca hallii* on the basis of the geographic distribution of taxa as presented by Pavlick and Looman (1984) and Harms (1985).

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[1] Scientific nomenclature follows Moss (1983) except where a different authority is cited in the text.

The sensitivity of fescue grasslands to defoliation has been noted since the early ecological survey work in Alberta (Moss and Campbell 1947). Where *Festuca-Stipa* grasslands have been inappropriately grazed, the canopy cover (%) and forage production of *Festuca hallii* has decreased (Bailey et al. 1988). Other studies have also indicated a season of defoliation effect with a greater vulnerability to spring defoliation than to autumn defoliation for *Festuca campestris* in south-central British Columbia and *Festuca hallii* in central Alberta (Bailey and Anderson 1978, McLean and Wikeem 1985). Therefore, there is indication of a period during the early growing season when *Festuca hallii* is especially sensitive to defoliation. The duration of this period of defoliation vulnerability for *Festuca hallii* within the *Festuca-Stipa* grasslands of central Alberta has not been established and therefore, an appropriate date of range readiness for grazing in this region has not been determined.

This study was a three-year (1985-1987) simulation of season of grazing effects on an undisturbed *Festuca-Stipa* range site in central Alberta. Single annual intense defoliations were applied with a rotary mower at the beginning of each month through the May to October growing season from 1985 to 1987. The purpose of this study was two-fold. The first purpose was to evaluate the effects of season of defoliation on the aboveground dry matter yield (DMY) and sward composition (DM%) of this *Festuca-Stipa* grassland. The second purpose was to evaluate the specific effects of season of defoliation on the inflorescence density, tiller density, and the end-of-season: stem base DM weight, stem base total nonstructural carbohydrates (TNC) percentage, stem base TNC pool and root DM weight of the key species, *Festuca hallii*.

MATERIALS AND METHODS

Study Area and Experimental Design

The study area (53°N latitude and 112°W longitude) was located on Section 28 of the University of Alberta's research ranch approximately 150 km southeast of Edmonton, Alberta. The climate is a cold-temperate Boreal climate (Walter 1985) with an average annual temperature of 1.9° C and a total average annual precipitation of 432 mm, of which 323 mm or 75% falls mostly as rain between April and September. Elevation is approximately 700 m above sea level. The grassland soils are predominantly thin Orthic Black

Chernozems (Howitt 1988). The grazing season is traditionally from May to December depending on the species being grazed and year-to-year differences in precipitation and snow cover.

The study area is on the northern edge of the grassland ecoclimatic province in Canada. It is a transitional zone between the more arid prairie to the south and the moister boreal forest to the north (Ecoregions Working Group 1989). Undisturbed areas are characterized by a mosaic of *Populus tremuloides* groves and *Festuca hallii* grasslands. Groves of trees occur on the moister sites with shrub and grassland communities on the drier sites. Shrub communities are dominated by *Amelanchier alnifolia*, *Elaeagnus commutata*, *Rosa acicularis*, *Rosa woodsii* and *Symphoricarpos occidentalis*. *Festuca hallii* dominates open undisturbed sites but *Stipa curtiseta* co-dominates on grazed sites (Wheeler 1976). Recent research indicates that *Festuca hallii* is also the dominant in autumn grazed areas (Bailey et al. 1988). Other grasses characteristic of the area depending on site, aspect, moisture and disturbance include; *Agropyron smithii*, *Agropyron trachycaulum*, *Agrostris scabra*, *Bouteloua gracilis*, *Festuca saximontana*, *Koeleria macrantha*, *Helictotrichon hookeri* and *Poa pratensis*. *Artemisia frigida* was a characteristic woody increaser on disturbed sites.

The specific study site was a 22.5 ha wedge of the aspen parkland mosaic, consisting of grassland (3.4 ha or 21%) and aspen forest and shrubs (17.8 ha or 79%), running north to south on the east side of Carrier Lake. This site was located within the boundaries of the University of Alberta Ranch, and had not been grazed for about 25 years. Ten blocks (20 X 40 m) within the ungrazed grassland area were created using a prescribed burn to remove the heavy accumulation of litter at the beginning of May, 1985. Control plots (2 X 10 m) in the ungrazed grassland were established adjacent to each burnt block. Randomized plots (2 X 10 m) for a burnt control, and single annual May, June, July, August, September and October defoliation treatments were established within each block.

Sward Dry Matter Yield

Total aboveground dry matter yield (DMY) was determined for the sward as a whole and the sward components of: *Festuca hallii,* other grasses and grass-like species, forbs, and woody species for the May, June, July, August, September and October defoliation treatments. The aboveground biomass yield was determined for each defoliation treatment by cutting a 600 cm by 52 cm strip at a height of 3 cm with an Arien 21" self-propelled rotary mower (McGinnies 1959). One side of each treatment plot was randomly selected for the mowing of the yield strip. The opposite side of each treatment plot was used for placement of 0.25-m^2 (25 X 100 cm) quadrats for sampling sward composition (%), inflorescence density and tiller density. The entire 2 X 10 m treatment plot was defoliated each time a treatment was applied with the rotary mower at height of 3 cm. The yield samples were placed in paper bags, air dried, and sifted with a 4.8 mm (6/32") rice sieve to remove litter and soil contaminants mixed with the forage sample resulting from the rotary mower's suction. The sifted samples were oven-dried at 65° C to a constant weight to determine aboveground dry matter yield (DMY). Dry matter yields of *Festuca hallii*, other grasses and grass-like species, forbs, and woody species were calculated based on their sward composition of each treatment plot for the samples collected by the rotary mower.

There was an insufficient area of grassland associated with the 10 blocks to permit the mowing of yield strips from the control and burnt control treatments each time a May to October season of defoliation treatment was applied. Therefore no sward DMY data were collected from the control and burnt control treatments using the rotary mower.

The season of defoliation treatment and sampling schedule is summarized in Table 4.1.

Sward Composition (DM%)

Sward composition was determined for the sward components of: *Festuca hallii*, other grasses and grass-like species, forbs, and woody species for the control, burnt control, May, June, July, August, September, and October defoliation treatments. Each treatment within a block was sampled for sward composition using two randomly located 0.25-m^2 (25 X 100 cm) quadrats placed on the opposite side to the production mowing strip. These quadrats were

Table 4.1 Date of May, June, July, August, September, and October season of defoliation treatments and date of collection of sward composition, inflorescence density, tiller density, and stem base core samples for 1985, 1986, and 1987.

		Date of sampling					
		May	Jun	Jul	Aug	Sep	Oct
1985	Defoliations	3[1]	3	3	2	3	5
1986	Defoliations	6	4	8	7 - 8	2	5
	Sward composition[2]	5	3	7	6 - 7	1	3
	Inflorescence density[3]		18				
	Tiller density[3]		18-20				
	Stem base cores[3]						10
1987	Defoliations	5	3	5	4	4	2 - 3
	Sward composition[2]	5	3	29 - 1	4	4	2 - 3
	Inflorescence density[3]		22-23				
	Tiller density[3]		22-24				
	Stem base cores[3]						2 - 3

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[1] The May 3, 1985 defoliation was a prescribed burn to remove litter from all blocks and all treatments except the control treatment.

[2] The sward composition for the control and burnt control treatments was sampled at the same time as the sward composition for the July season of defoliation treatment.

[3] All treatments sampled on dates indicated.

permanently placed for the May, June, July, August, September and October defoliation treatments. The quadrats were randomly reselected in 1987 in each of the controls and burnt controls in order to sample unclipped vegetation in both 1986 and 1987. The aboveground biomass was hand-clipped and separated into *Festuca hallii,* other grasses and grass-like species, forbs, woody, and litter components. For the May, June, July, August, September and October treatments, this clipping was done immediately prior to mowing of the production strip (Table 4.1). For the control and burnt control, the sward composition samples were collected prior to the July defoliation treatment. The sward composition samples were oven-dried at 65° C to a constant weight. Sward composition was calculated based on the relative DM weight of *Festuca hallii*, other grass and grass-like species, forbs, and woody components after deducting the litter component from the quadrats for each plot. The sward composition of *Festuca hallii*, other grasses and grass-like species, forbs, and woody components for each defoliation treatment plot was used to calculate their yield in each production strip.

Inflorescence Density

The *Festuca hallii* inflorescence density was determined on June 18, 1986 and June 22 and 23, 1987 by counting the *Festuca hallii* inflorescences in two randomly located 0.5-m^2 (50 X 100 cm) quadrats placed on the opposite side to the production mowing strip within each treatment plot. These quadrats were permanently located in the May, June, July, August, September and October defoliation treatments. The quadrats for the control and burnt control treatments were randomly reselected in 1987 in order to sample undisturbed vegetation in both 1986 and 1987.

The May and June season of defoliation treatments were defoliated prior to the inflorescence density data being collected at the end of June in 1986 and 1987. Therefore statistical analysis was performed for the control, burnt control, July, August, September and October treatments only.

Tiller Density

The *Festuca hallii* tiller density was determined in late June by counting the *Festuca hallii* tillers in 4 randomly located 0.04-m^2 quadrats placed on the opposite side to the production mowing strip within each treatment. The 0.04-m^2 quadrat size was determined by using the Two-Term Local-Quadrat Variance (TTLQV) method in order to minimize sampling variance (Ludwig, 1979). These quadrats were permanently located in the May, June, July, August, September and October defoliation treatments. The quadrats were randomly reselected in 1987 in the controls and burnt controls in order to sample unclipped vegetation in 1986 and 1987.

End-of-season Stem Base Weight, TNC (%), TNC Pool, and Root Weight

The *Festuca hallii* stem base weight, total nonstructural carbohydrate percentage (TNC (%)) and TNC pool were determined by removing four 7.0 cm diameter by 7.5 cm deep cores from each plot on October 10, 1986 and October 2-3, 1987. The cores were immediately placed in plastic bags, sealed, transported to a freezer, and frozen within thirty-six hours of extraction from the ground. Prior to analysis, the samples were thawed overnight at room temperature. The foliage was trimmed to 2 cm above the soil surface. The cores were washed and broken apart under cool tap water over a 2 mm screen to remove soil from the roots. During the washing process, the non-*Festuca hallii* species were separated and discarded. The *Festuca hallii* stem bases and roots were separated by trimming 2 to 4 mm below the interface of the stem base and roots. Rhizomes were retained with the stem bases. The stem base and root samples were oven-dried at 65° C to a constant weight and weighed. The root samples were then discarded. The stem base samples were ground using a Udy cyclone mill (1 mm screen). The ground stem base samples were frozen until later analysis.

Prior to TNC analysis, the stem base samples were removed from the freezer and dried overnight to a constant weight at 65° C and then stored in a desiccator. Stem base TNC (%) was determined with an acid hydrolysis technique. The technique was adapted from Smith (1981) in consultation with M. J. Trlica (personal communication, February 1987) and J. Richards (personal communication, May 1987). Duplicate 100 mg samples were refluxed for each treatment in 6 mls of 0.2N H_2SO_4 for one hour in a marble capped 25 X 200 mm test tube enclosed in a boiling water bath. The amount of TNC in each sample was determined by the Schaeffer

Somorgyi copper-iodometric titration technique as outlined by Smith (1981).

The end-of-season stem base TNC pool (g m^{-2}) was determined by multiplying the end-of-season stem base weight (g m^{-2}) by the end-of-season TNC (%).

Statistical Analysis

Data were analyzed by analysis of variance. Analysis of aboveground DMY was limited to the May, June, July, August, September and October defoliation treatments. All other analyses included the controls and burnt controls with the six monthly defoliation treatments. Multiple comparisons were made using Bonferroni's method which determined significant differences ($P<0.05$) simultaneously between treatments within a year and between years for a treatment (Milliken and Johnson 1984, T. Taerum, personal communication, January 1989). When there was no significant ($P>0.05$) year or defoliation treatment-by-year interaction, treatment results for the two years were averaged and analyzed with a one-way analysis of variance and the treatment means were separated using Student-Newman-Keuls multiple means test to determine significant differences ($P<0.05$). Percentage data were analyzed with and without a Box-Cox transformation (Sokal and Rohlf, 1981). Both transformed and untransformed data sets gave the same significant analysis of variance and multiple means separation.

RESULTS

Sward Dry Matter Yield

The total sward dry matter yield (DMY) had a season of defoliation-by-year interaction ($P<0.001$), a year-to-year effect ($P<0.001$), and a season of defoliation response ($P<0.001$) (Table 4.2).

The total sward DMY treatment average of 170 g m^{-2} in 1986 was higher ($P<0.001$) than the 137 g m^{-2} for 1987 (Table 4.2). This year-to-year effect was likely associated, in part, with differences between the annual accumulated precipitation to the end of September which, in 1986 was 345.7 mm (91% of normal), and for 1987 was 317.3 mm (83% of normal) (Table 2.3).

Timing of precipitation during the growing season would also have contributed to the year-to-year differences ($P<0.001$), and to the season of defoliation-by-year interaction ($P<0.001$) (Tables 2.2, 2.3, 4.2). The accumulated precipitation to the end of May was about the same for both years with 86.3 mm (71% of normal) in 1986 and 88.8 mm (74% of normal) in 1987. The major 1986-to-1987 precipitation timing differences were 60.4 mm (78% of normal) in contrast to 33.8 mm (43% of normal) for June, 115.5 mm (134% of normal) in contrast to 83.9 mm (97% of normal) for July, and 62.7 mm (168% of normal) in contrast to 31 mm (83% of normal) for September. These year-to-year precipitation timing differences correspond to the higher ($P<0.05$) total sward DM yields in 1986

Table 4.2 Mean square values of aboveground dry matter yield for the total sward, *Festuca hallii*, other grasses and grass-like species, forbs, and woody species in the May, June, July, August, September, and October defoliation treatments for 1986 and 1987.

Source	df	Total sward	*Festuca hallii*	Other grasses and grass-like species	Forbs	Woody species
Block (B)	9	4876 ***	1504	1475 **	4347 ***	9.3
Defoliation (D)	5	16821 ***	1256	1277 *	4330	15.8
Error 1 (B x D)	45	739	1154	401	874	10.9
Years (Y)	1	32822 ***	19324 ***	74	885 *	14.8 *
Error 2 (B X Y)	9	384	204	90	146	2.5
D X Y	5	2467 ***	2767 *	364 **	501 **	3.7
Error 3 (B x D x Y)	45	397	202	89	104	2.2

*, **, and *** indicate significant variances for $P < 0.05$, 0.01, and 0.001, respectively.

compared to 1987 for the July, August and October defoliation treatments (Table 4.3, Figure 4.1).

The total sward DMY for the May defoliation treatment was lower ($P<0.05$) than all the other season of defoliation treatments in both years (Table 4.3, Figure 4.1). This would contribute to the strong season of defoliation effect ($P<0.001$), despite the influence of the defoliation-by-year interaction ($P<0.001$) (Table 4.2).

Within years, the 1986 August defoliation treatment had a higher ($P<0.05$) total sward DMY than the June, July, September and October defoliation treatments (Table 4.3, Figure 4.1). This August response was likely a direct result of the July precipitation being 134% of normal in 1986 (Table 2.2). In contrast, there were no differences in 1987 among the total sward DM yields for the June-to-October defoliation treatments. These year-to-year differences in the season of defoliation effects would therefore contribute to the season of defoliation-by-year interaction ($P<0.001$) for the total sward DMY (Table 4.2).

The *Festuca hallii* DMY also had a season of defoliation-by-year interaction ($P<0.05$) and a year-to-year effect ($P<0.001$), but no ($P>0.05$) season of defoliation response when data was averaged over both years (Table 4.2).

The DMY treatment average for *Festuca hallii* in 1986 of 104 g m^{-2} was higher ($P<0.001$) than the 78 g m^{-2} for 1987 (Table 4.2). Again, this year-to-year effect was probably associated with the

Table 4.3 Aboveground dry matter yield of the total sward in the May, June, July, August, September and October defoliation treatments for 1986 and 1987.

	Aboveground DM yield (g.m^{-2})			
	1986		1987	
Season of defoliation treatment	Mean	SE	Mean	SE
May	107 c	10	93 b	7
June	182 b	13	165 a	7
July	179 b*	7	149 a*	8
August	219 a*	12	144 a*	9
September	163 b	9	141 a	6
October	169 b*	9	130 a*	14

The same letter following means within a column indicates no significant difference (Bonferroni; $P<0.05$).
An * indicates a significant difference between years for that treatment (Bonferroni; $P<0.05$).

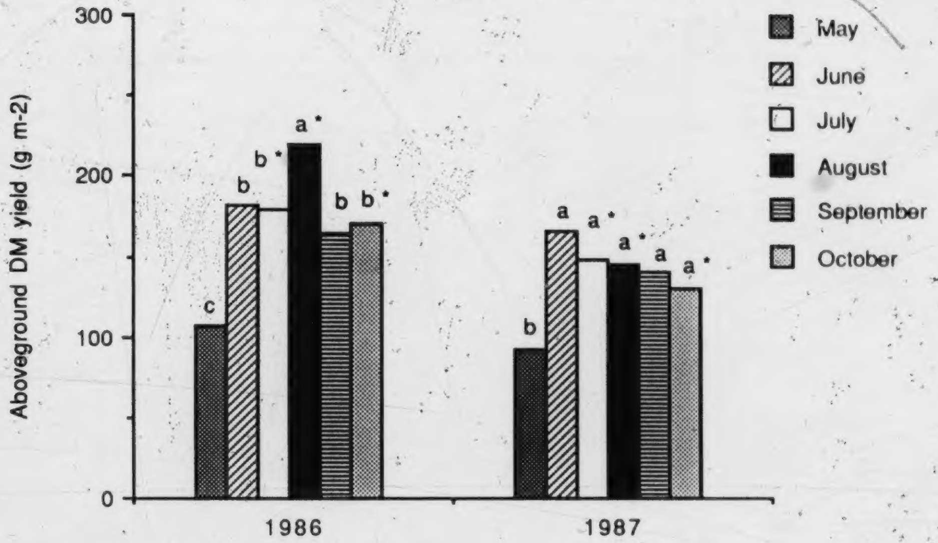

Figure 4.1 Aboveground dry matter (DM) yield of the sward by season of defoliation treatment for 1986 and 1987. Different letters above bars indicate significant differences among treatments within each year (P<0.05). An * indicates a significant difference between years for that treatment (P<0.05).

differences between the annual accumulated precipitation and the timing of precipitation during the growing season as noted above.

The *Festuca hallii* DMY for the August and September defoliation treatments were higher (P<0.05) in 1986 than in 1987 (Table 4.4, Figure 4.2). These year-to-year DMY differences corresponded with the higher than normal precipitation for July (134%) and September (168%) in 1986 (Table 2.2). The season of defoliation DMY differences (P<0.05) within 1986 would also contribute to the defoliation-by-year interaction (P<0.05) for *Festuca hallii*, as there were no (P>0.05) differences in DMY among the season of defoliation treatments in 1987.

The other grass and grass-like species DMY had a season of defoliation-by-year interaction (P<0.01) and a season of defoliation response (P<0.05), but no (P>0.05) year-to-year effect (Table 4.2).

The other grasses and grass-like species DMY for the June defoliation treatment was higher (P<0.05) than the May defoliation treatment in 1987 (Table 4.4). There were no (P>0.05) defoliation treatment differences in 1986. The defoliation treatment DMY differences within 1987, but not 1986, would contribute to the season of defoliation-by-year interaction (P<0.01) for the other grasses and grass-like species (Table 4.2).

The other grasses and grasslike species may have been more tolerant of the 1986-to-1987 precipitation differences than *Festuca*

Table 4.4 Aboveground dry matter yield of *Festuca hallii*, other grasses and grass-like species, forbs, and woody species in the May, June, July, August, September, and October defoliation treatments for 1986 and 1987.

		Aboveground DM yield ($g.m^{-2}$)			
		1986		1987	
Sward component	Defoliation treatment	Mean	SE	Mean	SE
Festuca hallii	May	82^{b}	7	72^{a}	6
	June	97^{ab}	8	90^{a}	5
	July	96^{ab}	10	86^{a}	9
	August	125^{a*}	12	76^{a*}	10
	September	98^{ab}	8	82^{a}	7
	October	126^{a*}	8	64^{a*}	8
Other grasses & grass-like species	May	14^{a}	6	7^{b}	3
	June	30^{a}	8	31^{a}	6
	July	35^{a}	8	26^{ab}	8
	August	32^{a}	7	23^{ab}	3
	September	17^{a}	5	18^{ab}	5
	October	16^{a}	4	30^{ab}	5
Forbs	May	10^{c}	7	14^{a}	3
	June	55^{b}	13	44^{a}	9
	July	48^{b}	12	36^{a}	9
	August	61^{a*}	12	44^{a*}	10
	September	45^{b}	8	39^{a}	8
	October	26^{bc}	6	36^{a}	7
Woody species	May	0.5^{a}	0.3	0.4^{a}	0.2
	June	0.5^{a}	0.3	0.4^{a}	0.2
	July	1.1^{a}	0.8	0.7^{a}	0.5
	August	1.5^{a}	1.5	0.9^{a}	0.9
	September	3.9^{a}	1.6	1.5^{a}	0.9
	October	0.5^{a}	0.2	0.0^{a}	0.0

The same letter following means within columns for sward components indicates no significant difference (Bonferroni; $P<0.05$).
An * indicates a significant difference between years for that treatment (Bonferroni; $P<0.05$).

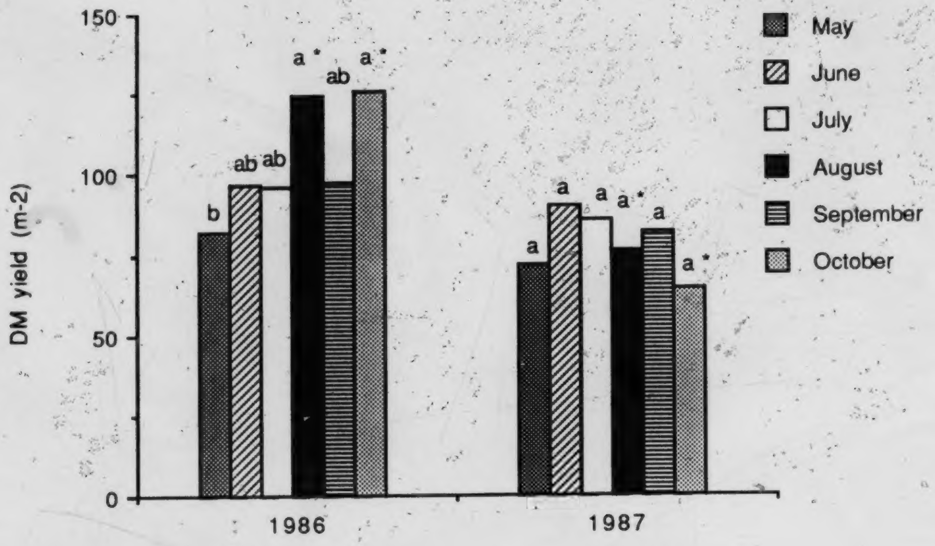

Figure 4.2 Aboveground dry matter (DM) yield of *Festuca hallii* by defoliation treatment for 1986 and 1987. Different letters above bars indicate significant differences among treatments within each year ($P<0.05$). An * indicates a significant difference between years for that treatment ($P<0.05$).

hallii, as there was no ($P>0.05$) year-to-year effect on their DMY (Table 4.2).

The forb DMY had a season of defoliation-by-year interaction ($P<0.01$) and a year-to-year effect ($P<0.05$), but no ($P>0.05$) season of defoliation response when the data was averaged over both years (Table 4.2).

The DMY treatment average for the forbs of 41 g m^{-2} in 1986 was higher ($P<0.001$) than the 35 g m^{-2} for 1987 (Table 4.2). Once again, this year-to-year effect was probably associated with the differences between the annual accumulated precipitation and the timing of precipitation during the growing season.

The forb DMY for the August defoliation treatments was higher ($P<0.05$) in 1986 than in 1987 (Table 4.4). Again, this year-to-year DMY difference corresponded with the higher than normal precipitation for July (134%) in 1986 (Table 2.2). The defoliation treatment DMY differences ($P<0.05$) within 1986, but not 1987 ($P>0.05$), would likely have contributed to the season of defoliation-by-year interaction ($P<0.01$) for the forb DMY (Table 4.2).

The woody species DMY had a year-to-year effect ($P<0.05$), but no season of defoliation response ($P>0.05$) nor season of defoliation-by-year interaction ($P>0.05$) (Table 4.2).

The DMY treatment average for the woody species of 1.3 g m^{-2} in 1986 was higher ($P<0.001$) than the 0.6 g m^{-2} for 1987 (Table

4.2). There was no apparent association with the year-to-year precipitation patterns and the DMY of the woody species as there was no (P>0.05) season of defoliation differences, nor any season of defoliation-by-year interaction (P>0.05) for the DMY of woody species. The magnitude of the 1986-to-1987 year effect on aboveground DMY increased as the growing season progressed. These 1986-to-1987 differences by season of defoliation treatment were; 20% for May and June, 36% for July, 40% for August, 62% for September, and then 100% for October. These results need to be taken with caution, however, given the small values that the woody species represent in the aboveground DMY of the sward as a whole, and an inadequate homogeneity of variance for a reliable analysis of variance for the woody species component.

Sward Composition

The *Festuca hallii* sward composition (DM%) had a season of defoliation-by-year interaction (P<0.001), a year-to-year effect (P<0.05), and a season of defoliation response (P<0.01) when data was averaged over both years (Table 4.5).

The sward composition average for *Festuca hallii* in 1986 of 64.1% was higher (P<0.05) than the 60.4% for 1987 (Table 4.5). This year-to-year effect on sward composition was probably associated with the 1987 *Festuca hallii* DMY being lower (P<0.001) than in 1986 (Table 4.2).

Table 4.5 Mean square values of sward composition for *Festuca hallii*, other grasses and grass-like species, forbs, and woody species in the control, burnt control, May, June, July, August, September, and October defoliation treatments for 1986 and 1987.

Source	df	*Festuca hallii*	Other grasses and grass-like species	Forbs	Woody
Block	9	879 *	505 ***	1481 ***	9.1
Defoliation (D)	7	1237 **	444 **	596	33.8 ***
Error 1 (B x D)	63	384	124	318	7.5
Years (Y)	1	532 *	121	159	1.6 *
Error 2 (B x Y)	9	99	60	72	2.7
D X Y	7	462 ***	163 ***	109	1.7
Error 3 (B x D x Y)	63	67	31	54	1.6

*, **, and *** indicate significant variances for $P< 0.05$, 0.01, and 0.001, respectively.

The *Festuca hallii* sward composition for the October defoliation treatments was higher ($P<0.05$) in 1986 at 74.7% than in 1987 at 49.1% (Table 4.6, Figure 4.3). These sward composition values were the highest and lowest values for 1986 and 1987, respectively, and corresponded to the highest and lowest DMY values for those years as well (Table 4.4, Figure 4.2). As noted in the previous section, the peak *Festuca hallii* DMY in 1986 under the October defoliation treatment was likely associated with the precipitation for September being 168% of normal for that year (Table 2.2). This extreme year-to-year swing in the sward composition values for the October defoliation treatment would also contribute to the strong defoliation-by-year interaction ($P<0.001$) for the *Festuca hallii* sward composition (Table 4.5). This interaction appears to be largely a function of the effect of timing of above, or below, normal amounts of precipitation on the subsequent DMY of *Festuca hallii* within each year.

Multiple means separation for *Festuca hallii* sward composition indicated that none ($P>0.05$) of the season of defoliation treatments were different from the control or burnt control in either year (Table 4.6, Figure 4.3). The *Festuca hallii* sward composition for the May defoliation treatment had the highest ($P<0.05$) value for both years which would contribute to the season of defoliation effect ($P<0.01$) (Tables 4.5). The May defoliation treatment sward composition was higher ($P<0.05$) than the June and July defoliation treatments in 1986, and higher ($P<0.05$) than the

Table 4.6 Sward composition of *Festuca hallii*, other grasses and grass-like species, forbs, and woody species in the control, burnt control, May, June, July, August, September, and October defoliation treatments for 1986 and 1987.

		Sward composition (DM%)			
	Defoliation	1986		1987	
Sward component	treatment	Mean	SE	Mean	SE
Festuca hallii	Control	70.1 ab	4.2	64.4 ab	5.5
	Burnt control	62.3 ab	7.5	66.5 ab	5.9
	May	78.6 a	4.0	78.0 a	3.9
	June	54.5 b	4.7	55.3 ab	3.5
	July	54.8 b	6.5	58.9 ab	6.5
	August	57.7 ab	5.0	52.3 b	5.4
	September	59.8 ab	4.9	58.8 ab	5.0
	October	74.7 ab*	3.6	49.1 b*	2.8
Other grasses & grass-like species	Control	5.2 b	2.2	6.8 b	2.2
	Burnt control	10.6 ab	3.2	7.8 b	2.1
	May	11.2 ab	4.2	7.4 b	2.8
	June	16.4 ab	4.0	18.6 b	3.4
	July	19.2 a	4.0	16.9 b	4.3
	August	15.6 ab	3.6	17.3 b	2.9
	September	9.7 ab	2.4	12.4 b	3.2
	October	10.0 ab*	2.1	24.4 a*	3.6
Forbs	Control	21.0 a	4.1	24.4 a	6.0
	Burnt control	25.6 a	7.1	24.3 a	5.6
	May	9.7 a	1.7	13.4 a	2.1
	June	28.9 a	5.5	25.8 a	4.3
	July	25.4 a	6.3	23.8 a	5.8
	August	26.2 a	4.5	29.9 a	6.2
	September	28.0 a	5.7	27.6 a	5.7
	October	15.1 a	3.5	26.5 a	3.9
Woody	Control	3.7 a	1.2	4.4 a	1.4
	Burnt control	1.6 ab	0.9	1.3 ab	0.6
	May	0.5 b	0.3	0.4 b	0.2
	June	0.3 b	0.2	0.3 b	0.2
	July	0.6 b	0.4	0.3 b	0.3
	August	0.6 b	0.6	0.5 b	0.5
	September	2.6 ab	1.1	1.2 ab	0.8
	October	0.3 b	0.1	0.0 b	0.0

The same letter following means within columns for sward components indicates no significant differences (Bonferroni; $P<0.05$).

An * indicates a significant difference between years for that treatment (Bonferroni; $P<0.05$).

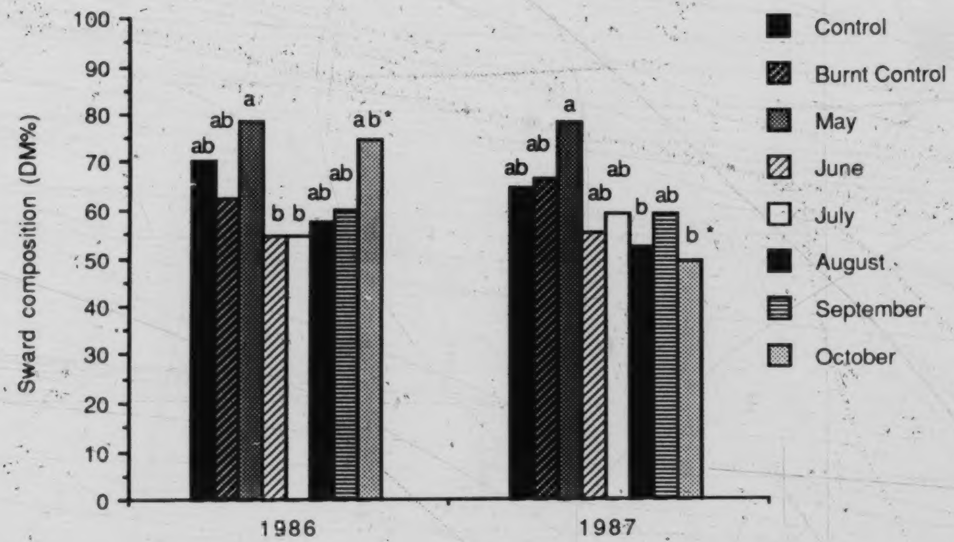

Figure 4.3 Sward composition of *Festuca hallii* by defoliation treatment for 1986 and 1987. Different letters indicate significant differences within years ($P<0.05$). An * indicates a significant difference between years for that treatment ($P<0.05$).

August and October defoliation treatments in 1987. The year-to-year shift in which season of defoliation treatment would have a lower ($P<0.05$) sward composition value than the May defoliation treatment would also contribute to the strong season of defoliation-by-year interaction ($P<0.001$) for *Festuca hallii* sward composition (DM%).

The other grass and grass-like species sward composition had a season of defoliation-by-year interaction ($P<0.001$) and a season of defoliation response ($P<0.01$), but no ($P>0.05$) year-to-year effect (Table 4.5).

Only the other grasses and grass-like species sward composition for the July defoliation treatment was higher ($P<0.05$) than the control in 1986 (Table 4.6). In contrast, the sward composition for the October defoliation treatment was higher ($P<0.05$) than all the other treatments in 1987. There was a year-to-year difference under the October defoliation treatment with the sward composition higher ($P<0.05$) in 1987 than in 1986. The 1986-to-1987 increase ($P<0.05$) in the other grass and grass-like species sward composition for the October defoliation treatment with no ($P>0.05$) corresponding year-to-year difference in their DMY, likely reflected the parallel, and sharp decrease, in the DMY and sward composition of *Festuca hallii* for the 1987 October defoliation treatment. The year-to-year changes in which defoliation treatments had sward composition differences would also have contributed to the strong season of defoliation-by-year interaction

(P<0.001) for the sward composition of the other grasses and grasslike species (Table 4.5).

The other grasses and grasslike species appear to have been more tolerant of the overall 1986-to-1987 precipitation and DMY differences than *Festuca hallii*, as there was no (P>0.05) year-to-year effect on their sward composition (Table 4.5).

The forb sward composition had no (P>0.05) season of defoliation-by-year interaction, nor year-to-year effect, nor season of defoliation response when the data was averaged over both years (Table 4.5). This suggests that across all treatments over both years their sward composition was relatively stable at 23.5% (Table 4.6). This apparent stability in sward composition for the forbs was independent of their year-to-year differences (P<0.05) in DMY (Table 4.4). This may be related to the forbs following a similar DMY pattern to *Festuca hallii* in response to the year-to-year differences in amounts and timing of precipitation.

The woody species sward composition had a year-to-year effect (P<0.05) and a season of defoliation response (P<0.001), but no season of defoliation-by-year interaction (P>0.05) (Table 4.5).

The sward composition treatment average for the woody species of 1.3% in 1986 was higher (P<0.05) than the 1.0% for 1987 (Table 4.5). There was no apparent association with the year-to-year precipitation patterns and the DMY of the woody species as there was no ($P>0.05$) season of defoliation differences, nor any season of defoliation-by-year interaction ($P>0.05$).

The woody species sward composition for the control treatment was higher ($P<0.05$) for both years than the May-to-August and October season of defoliation treatments (Table 4.6). This suggests that the combination of the May 1985 burn and the 1985-to-1987 annual defoliations by mowing, with the exception of the September defoliation treatment, reduced ($P<0.05$) the woody species sward composition compared to the control. There was no ($P>0.05$) parallel reduction in woody sward composition for the same season of defoliation treatments when compared to the burnt control.

The results for the woody species sward composition need to be taken with caution, however, given the small values that the woody species represent in the sward composition of the sward as a whole, and an inadequate homogeneity of variance for a reliable analysis of variance for the woody species component.

Inflorescence Density

The inflorescence density of *Festuca hallii* had a season of defoliation-by-year interaction ($P<0.001$) and a season of defoliation response ($P<0.01$), but no ($P>0.05$) year-to-year effect (Table 4.7).

Table 4.7 Mean square values of the inflorescence density of *Festuca hallii* in the control, burnt control, July, August, September, and October defoliation treatments for 1986 and 1987.

Source	df	Inflorescence density
Block (B)	9	2366
Defoliation (D)	5	5449 **
Error 1 (B x D)	45	1166
Years (Y)	1	4165
Error 2 (B x Y)	9	2701
D X Y	5	5026 ***
Error 3 (B x D x Y)	45	785

, and * indicate significant variances for $P < 0.01$, and 0.001, respectively.

The low May and June values were due, in part, to the inflorescence density sampling date being at the end of June which was approximately seven and three weeks, respectively, after the application of those treatments (Table 4.8, Figure 4.4). Therefore, data for these treatments were not included in the statistical analysis, but their values were recorded.

The inflorescence density for *Festuca hallii* for the burnt control and the October defoliation treatment were higher ($P<0.05$) than the July and August defoliation treatments in 1987 (Table 4.8, Figure 4.4). There were no ($P>0.05$) inflorescence density differences among defoliation treatments in 1986. The inflorescence density differences ($P<0.05$) among defoliation treatments within 1987, but not 1986, would contribute to the season of defoliation-by-year interaction ($P<0.001$) (Table 4.7). In 1987, inflorescence densities increased 25-fold for the control, but decreased 8-fold for the August treatment. This contrasting response among treatments within 1987 would also contribute to the strong season of defoliation-by-year interaction ($P<0.001$).

Tiller Density

Tiller density was affected ($P<0.001$) by the season of defoliation treatments, but there were no ($P>0.05$) season of defoliation-by-year interaction nor ($P>0.05$) year-to-year effect (Table 4.9).

Table 4.8 Inflorescence density of *Festuca hallii* in the control, burnt control, July, August, September, and October defoliation treatments for 1986 and 1987.

Season of defoliation treatment	n	Density (# m^{-2}) 1986 Mean		1987 Mean	
		Mean	SE	Mean	SE
Control	10	1.9 a	1.0	48.4 ab	10.8
Burnt control	10	45.9 a	18.9	56.7 a	11.2
May	10	1.7	0.7	0.1	0.1
June	10	0.0	0.0	0.0	0.0
July	10	10.4 a	3.4	4.1 b	2.9
August	10	47.1 a	13.9	5.8 b	2.7
September	10	26.7 a	9.5	49.4 ab	12.0
October	10	32.3 a	12.1	67.6 a	16.7

The same letter following means within columns indicates no significant difference (Bonferroni; $P<0.05$). The May and June treatments were not statistically compared as they were defoliated prior to the collection of the density data in 1986 and 1987.

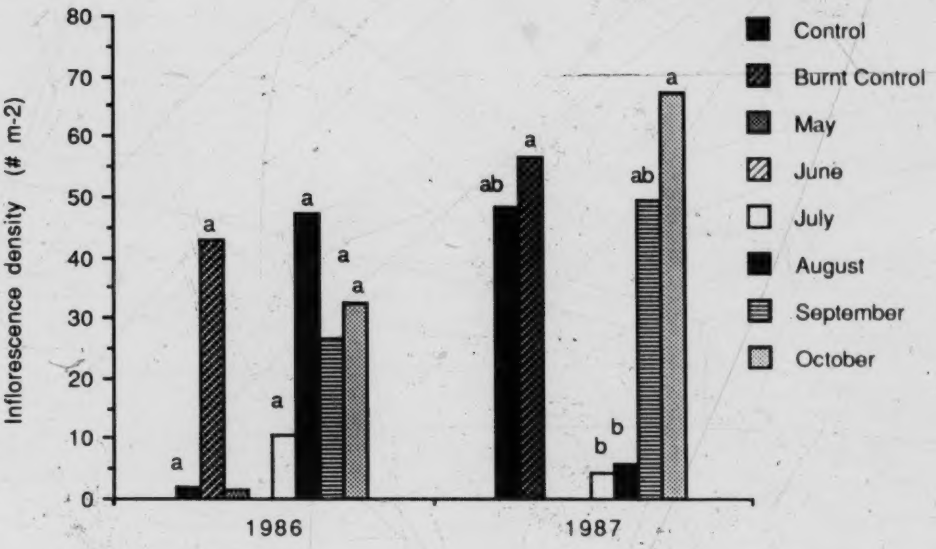

Figure 4.4 Inflorescence density (# m^{-2}) of *Festuca hallii* by defoliation treatment for 1986 and 1987. Different letters above bars indicate significant differences among defoliation treatments within each year (P<0.05). The May and June treatments were not statistically compared as they were defoliated prior to the collection of the density data in 1986 and 1987.

Table 4.9 Mean square values of tiller density, stem base dry matter (DM) weight, stem base total nonstructural carbohydrate (TNC) percentage, stem base TNC pool, and root DM weight to a 7.5 cm depth for *Festuca hallii* in the control, burnt control, May, June, July, August, September, and October defoliation treatments for 1986 and 1987.

Source	df	Tiller density	Stem base DM weight	Stem base TNC%	Stem base TNC pool	Root DM weight
Block (B)	9	2757800	61641 *	8.5 ***	1248 *	119982 **
Defoliation (D)	7	11202000 ***	19709	3.7 *	178	43558
Error 1 (B x D)	63	1496600	29023	1.4	508	40714
Years (Y)	1	705566	34563	61.4 **	3288 *	207360
Error 2 (B x Y)	9	1121600	16101	4.3	482	98048
D X Y	7	246933	20706	2.0	340	54150 *
Error 3 (B x D x Y)	63	278613	20852	1.0	340	24562

*, **, and *** indicate significant variances for $P < 0.05$, 0.01, and 0.001, respectively.

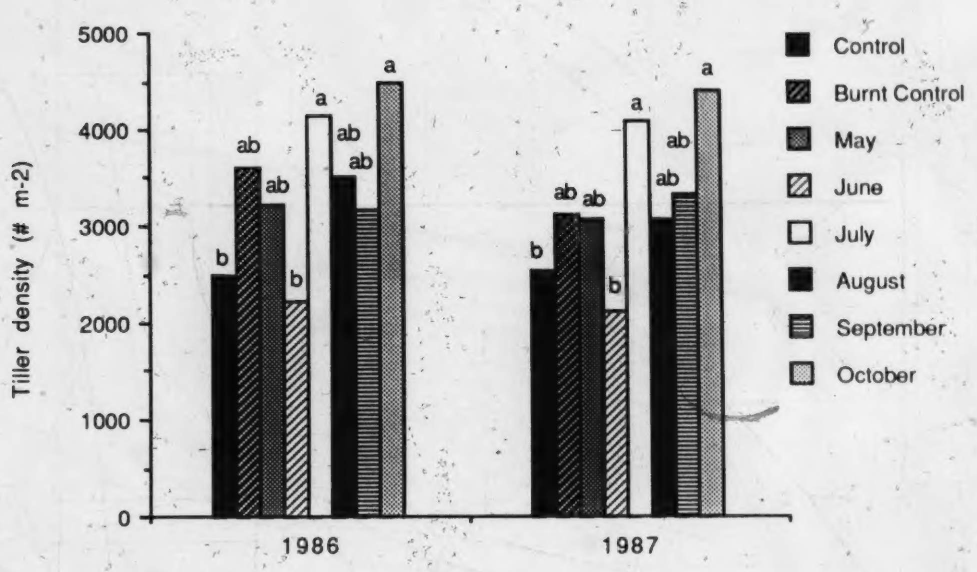

Figure 4.5 Tiller density (# m^{-2}) of *Festuca hallii* by defoliation treatment for 1986 and 1987. Different letters above bars indicate significant differences among defoliation treatments within each year ($P<0.05$).

Plants from the control and June defoliation treatments had fewer ($P<0.05$) tillers than plants from the July and October defoliation treatments in both years (Figure 4.5). As there was no significant year-to-year effect or defoliation treatment-by-year interaction, the results of the two years were averaged and reanalyzed using a one-way analysis of variance with the means separated by the Student-Newman-Keuls technique. Using this analysis, only plants from the June defoliation treatment had lower ($P<0.05$) tiller densities than those in the burnt control, July and October defoliation treatments (Table 4.10).

End-of-season Stem Base Weight, TNC (%), and TNC Pool

There were no ($P>0.05$) season of defoliation, year-to-year, or season of defoliation-by-year interaction effects for the end-of-season stem base DM weights (g m^{-2}) after three years of intense annual defoliations (Tables 4.9 and 4.11).

The end-of-season stem base TNC (%) had a year-to-year effect ($P<0.01$) and a season of defoliation effect ($P<0.05$), but no ($P>0.05$) season of defoliation-by-year interaction (Table 4.9).

The end-of-season TNC (%) of 13.9% in 1986 was higher ($P<0.01$) than the 12.6% in 1987 (Table 4.9). This year-to-year difference in end-of-season TNC (%) may have been associated with the degree of winter hardening as influenced by the average September temperature, which in 1986 was 8.5^o C (1.9^o C below normal), while in 1987 it was 13.3^o C (2.9^o C above normal) (Table

Table 4.10 Tiller density of *Festuca hallii* in the control, burnt control, May, June, July, August, September, and October defoliation treatments for the combined 1986 and 1987 data.

		Density (# m^{-2})	
Defoliation treatment	n	Mean	SE
Control	10	2509 cd	228
Burnt control	10	3361 bc	318
May	10	3155 bcd	304
June	10	2170 d	243
July	10	4115 ab	386
August	10	3291 bcd	311
September	10	3260 bcd	262
October	10	4453 a	209

The same letter following the means indicates no significant differences (Student-Newman-Keuls; $P<0.05$).

2.4). The end-of-season stem base TNC (%) in plants from the burnt control and September defoliation treatments were higher ($P<0.05$) in 1986 than in 1987.

Analysis of variance suggested a season of defoliation effect ($P<0.05$) for the end-of-season stem base TNC (%) (Table 4.9). The multiple means separation, however, indicated no defoliation treatment differences ($P>0.05$) for 1986 or 1987 (Table 4.11). The *Festuca hallii* plants in the May defoliation treatment had the highest TNC (%) value, while the plants in the June defoliation treatment had either the second or third highest TNC (%) values over both years. The *Festuca hallii* plants in the September defoliation treatment had either the lowest or second lowest TNC (%) values over both years. The similar ranking pattern of these three season of defoliation treatments for each year, even with no ($P>0.05$) significant differences among them within years, may have contributed to the suggested ($P<0.05$) season of defoliation effect.

The end-of-season stem base TNC pool (g m^{-2}) had a year-to-year effect ($P<0.01$) but no ($P<0.05$) season of defoliation effect nor ($P<0.05$) season of defoliation-by-year interaction (Table 4.9).

The end-of-season TNC pool of 54.0 g m^{-2} in 1986 was higher ($P<0.05$) than the 44.9 g m^{-2} in 1987 (Table 4.9). This year-to-year TNC pool (g m^{-2}) difference ($P<0.05$) would appear to be largely a function of the year-to-year difference ($P<0.01$) in TNC (%) as there was no ($P>0.05$) year-to-year, nor ($P>0.05$) season of defoliation differences for the end-of-season stem base DM weights (g m^{-2}) (Table 4.11).

Root Weight

The end-of-season *Festuca hallii* root weight (g m^{-2})) had a season of defoliation-by-year interaction ($P<0.05$) but no ($P>0.05$) year-to-year effect, nor ($P>0.05$) season of defoliation response (Table 4.9).

The overall average, of all treatments across both years, for the end-of-season root weight to a 7.5 cm depth was 553 g m^{-2}. The weights for the control and May defoliation treatments decreased in 1987 compared to 1986 (Table 4.12, Figure 4.6). In contrast, the weights for the burnt control and the June-to-October defoliation treatments all increased in 1987 compared to 1986. This contrast in treatment-by-treatment root DM weight changes from 1986-to-1987 would contribute to the season of defoliation-by-year interaction ($P<0.05$) (Table 4.9).

Table 4.11 End-of-season (October) stem base dry matter weight, stem base total nonstructural carbohydrate (TNC) percentage, and stem base TNC pool for *Festuca hallii* in the control, burnt control, May, June, July, August, September, and October defoliation treatments for 1986 and 1987.

Festuca hallii parameter	Defoliation treatment	n	1986		1987	
			Mean	SE	Mean	SE
			(g.m^{-2})			
Stem base DM weight	Control	10	393 a	57	310 a	31
	Burnt control	10	365 a	52	401 a	74
	May	10	401 a	47	314 a	26
	June	10	354 a	35	300 a	40
	July	10	407 a	71	385 a	48
	August	10	390 a	56	364 a	44
	September	10	476 a	76	387 a	48
	October	10	333 a	51	423 a	41
			(%)			
Stem base TNC %	Control	10	13.9 a	0.3	13.3 a	0.3
	Burnt control	10	14.1 a*	0.4	12.1 a*	0.3
	May	10	14.5 a	0.5	13.3 a	0.5
	June	10	13.9 a	0.5	13.2 a	0.6
	July	10	13.4 a	0.6	13.0 a	0.4
	August	10	13.7 a	0.5	11.9 a	0.3
	September	10	13.6 a*	0.4	11.7 a*	0.2
	October	10	13.8 a	0.5	12.5 a	0.3
			(g.m^{-2})			
Stem base TNC pool	Control	10	55 a	8.7	41 a	4.4
	Burnt control	10	51 a	6.3	47 a	7.1
	May	10	58 a	7.0	42 a	4.2
	June	10	49 a	5.5	40 a	5.4
	July	10	53 a	8.3	49 a	4.7
	August	10	54 a	8.5	43 a	5.1
	September	10	65 a	11.9	45 a	5.1
	October	10	47 a	8.5	53 a	5.1

The same letter following means within columns indicates no significant difference (Bonferroni; $P<0.05$).

An * indicates a significant difference between years for that treatment (Bonferroni; $P<0.05$).

Table 4.12 End-of-season (October) root dry matter weights to a 7.5 cm depth for *Festuca hallii* in the control, burnt control, May, June, July, August, September and October defoliation treatments in 1986 and 1987.

		1986		1987	
Defoliation treatment	n	Mean	SE	Mean	SE
		$(g.m^{-2})$			
Control	10	557 a	81	526 a	50
Burnt control	10	470 a	62	640 a	88
May	10	577 a	84	491 a	27
June	10	503 a	63	536 a	61
July	10	475 a	76	545 a	62
August	10	476 a	31	574 a	54
September	10	555 a	64	636 a	41
October	10	523 a	85	764 a	85

The same letter following means within columns indicates no significant difference (Bonferroni; $P<0.05$).

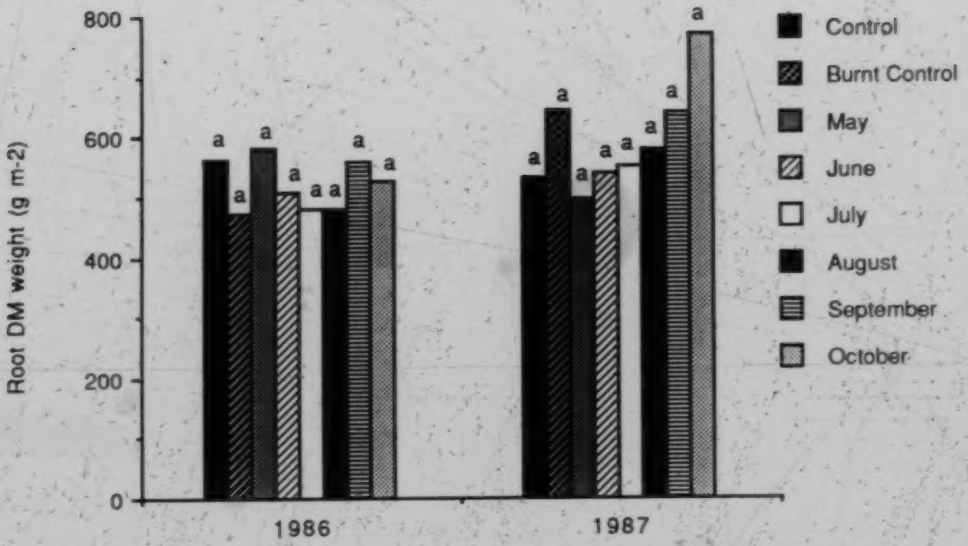

Figure 4.6 Root dry matter (DM) weight to a 7.5 cm depth for *Festuca hallii* by defoliation treatment in 1986 and 1987. Different letters above bars indicate significant differences among defoliation treatments within each year ($P<0.05$).

DISCUSSION

Sward Responses - Yield and Species Composition

The significant season of defoliation-by-year interactions for the aboveground DMY of the total sward, and each of the herbaceous components which were separated, suggested that timing of growing season precipitation had more influence than season of defoliation on aboveground DMY of the sward and its herbaceous components (Tables 4.2, 4.3, 4.4). It is important to note that for each season of defoliation treatment which had a significant year-to-year DMY difference (the sward DMY of the July, August, and October treatments, the *Festuca hallii* DMY for the August and October treatments, and the forb DMY of the August treatment) the month preceding the defoliation treatment had substantially greater precipitation in 1986 than in 1987 (Tables 2.3).

The year-to-year responsiveness of the *Festuca hallii* aboveground DMY for the August and October defoliation treatments to the annual differences in precipitation suggests that DM productivity for this species was moisture limited in both years (Figure 4.2). This is well illustrated with the monthly June-to-September precipitation amounts and the aboveground DM yields for the July-to-August defoliation treatments in 1986 (Tables 2.2, 4.4). The increase in the aboveground DMY for the October defoliation treatment compared to the September defoliation treatment in 1986 suggests that *Festuca hallii* has the capacity for late season growth if moisture is available. This DMY response to above average September moisture in 1986 helps to explain why the *Festuca hallii* sward composition increased during 1986 as the season progressed and was significantly higher in 1986 compared to 1987 for the October defoliation treatment (Figure 4.3).

The forb DMY appeared to be less responsive to late season moisture than the DMY of *Festuca hallii* (Table 4.4). Only the forb DMY for the August defoliation treatment was higher ($P<0.05$) in 1986 compared to 1987 in response to the above average precipitation in July 1986 (Tables 2.2, 4.4). This suggests that the forb component of the sward could not utilize the late season precipitation as well as *Festuca hallii* did in 1986. This suggests that *Festuca hallii* may have a competitive advantage over the forbs in utilizing late season precipitation.

There was no ($P>0.05$) year-to-year effect on DMY for the other grasses and grass-like species component of the sward indicating that these species were not able to take any significant advantage of the year-to-year differences in amounts and timing of precipitation (Tables 2.2, 4.2, 4.3). This also suggests that the DMY of these species was not as sensitive to the year-to-year differences in precipitation as that of the forbs or *Festuca hallii*. It also suggests moisture was not limiting to the DM productivity of the other grasses and grass-like species in 1986 and 1987. This may indicate that the other grasses and grass-like species would not compete well with *Festuca hallii* when precipitation amounts were normal or better.

The only consistent season of defoliation effect was the lower ($P<0.05$) DMY of the total sward for the May defoliation compared to the other defoliation treatments (Tables 4.2, 4.3, Figure 4.1). Accumulated precipitation to the end of April and to the end of May was about the same for both years (Table 2.3). Therefore, the lower ($P<0.05$) total sward DMY for the May defoliation treatment compared to the June defoliation would likely reflect a season of defoliation treatment response independent of any year-to-year differences in timing of precipitation amounts as discussed earlier. The lower ($P<0.05$) DMY for the May treatment compared to the June treatment likely reflected the rapid growth of the sward components through the month of May compared to the more limited growth during the month of April (Chapter III).

Bailey and Anderson (1978) reported no season of defoliation effect for the total September herbage DMY following an early October versus an early May defoliation by fire on a *Festuca-Stipa* grassland near Kinsella, Alberta. This would suggest no immediate residual season of defoliation effect on the herbage DMY after a single treatment application.

There was no season of defoliation effect for the DMY results averaged over both years for the sward components of *Festuca hallii*, forbs, and woody species (Tables 4.2). For *Festuca hallii* this result was in contrast to other studies which have suggested that annual defoliations in late May and early June would suppress DMY compared to annual defoliations at other times of the year (Sinton and Bailey 1980, McLean and Wikeem 1985).

Sinton and Bailey (1980) examined the effects of three different spring defoliation treatments (April 8, April 27, June1), using fire or mowing, on *Festuca hallii* aboveground DMY. The DMY response to defoliation by mowing or burning was virtually identical. There was a trend for the aboveground regrowth DMY collected in August to decrease linearly for the April 8 to June 1 defoliation treatments. This suggests that the regrowth capacity of *Festuca hallii* was more vulnerable to defoliation in early June than early April, when measured by DMY in the following August. These results are consistent with the growth cycle patterns described in Chapter III. A defoliation on April 8th would be prior to the critical late April to early June growth period for *Festuca hallii*.

In this study the May DMY for *Festuca hallii* was lower than the June DMY in both years. This result also reflects the nature of the growth cycle of *Festuca hallii* in which a lower yield would be expected in early May just after spring growth initiation (Chapter III). In early June, a higher *Festuca hallii* DMY would be expected because of the rapid growth during the month of May.

McLean and Wikeem (1985) noted significantly lower total DMY for repeated weekly (5 cm) defoliations during May, compared to a single September defoliation in a three year study in south-central British Columbia on *Festuca campestris*. It would have been of interest to know whether their study would have still produced a significant May versus September DMY difference with only a single versus multiple May defoliations. They also showed that the mid-May to June defoliation period caused a significant reduction in DMY compared to defoliation in May only, suggesting that the mid-May to early June season was the more sensitive period for defoliation of *Festuca campestris*.

Allowing for the year-to-year differences in the amounts and patterns of precipitation, the results of this study indicated no clear season of defoliation treatment effect on the aboveground DMY of *Festuca hallii* except for what might be predicted from the nature of the *Festuca hallii* growth cycle (Chapter III). The results of the studies cited above and those of Chapter III suggest that the early June defoliation treatment was the most detrimental to the plant. However, after two years of treatment application in this study, an anticipated early June suppression of *Festuca hallii* aboveground DMY did not occur. This study would therefore suggest that more than two years of treatment application are needed to determine whether a single annual intense defoliation at the beginning of June will suppress *Festuca hallii* DMY because of the physiological vulnerability of the plant at that time in its growth cycle, compared to the same defoliation treatment during the other months of the growing season.

There was no ($P<0.05$) season of defoliation effect on the aboveground DMY of the forbs but they had a 3-to-5 fold increase in the aboveground DMY for the May-to-June season of defoliation treatments (Tables 4.2, 4.4). This likely reflected the comparatively delayed spring growth of the forbs compared to *Festuca hallii* (Chapter III).

There were no ($P<0.05$) differences among the aboveground DM yields of the season of defoliation treatments for the woody species (Tables 4.2, 4.4). However, for each treatment there was a reduction in the aboveground DMY in 1987 compared to 1986. The magnitude of this reduction was progressive through the growing season being 20% for May and June, 36% for July, 40% for August, and then 100% for October. This suggests that the longer defoliation was delayed in the growing season, the greater the impact of that defoliation on the woody species. This trend might be associated with the removal of carbohydrate reserves stored in the stems of the woody species. The later in the growing season that the woody species were defoliated, the greater the impact of the diminishing time available for regrowth and carbohydrate reserve restoration prior to overwintering. A study set up to look specifically at the woody species where greater precision in measurement of the woody species was emphasized might determine a significant season of defoliation effect.

There was a season of defoliation effect ($P>0.05$) on the aboveground DMY for the other grasses and grass-like species (Tables 4.2, 4.4). The aboveground DMY for the 1987 June treatment was higher ($P<0.05$) than the May treatment. A similar though not significant increase in aboveground DMY was observed for the May to June season of defoliation treatments in 1986. The low DMY of the other grasses and grass-like species for the May compared to June treatments was probably associated with an increased growth rate during May compared to April (Chapter III).

Given that there was no ($P>0.05$) season of defoliation treatment effects on *Festuca hallii* aboveground DMY, the drop in the June, July, August and September sward composition for *Festuca hallii* likely reflects the 2 to 5 fold increase in the aboveground DM yields of the other grasses and grass-like species and the forbs for the June, July, August and September defoliation treatments compared with the May treatment (Tables 4.2, 4.4, 4.5, 4.6). This probably reflects the delayed growth cycles of the other grasses and grass-like species and the forbs compared with *Festuca hallii* (Chapter III). The lack of significant defoliation treatment effects on *Festuca hallii* aboveground DMY may also help explain why none of the season of defoliation treatments were significantly different from the control and burnt control for sward composition (DM%). It is important to note, however, that this was a short three year study of a long lived perennial plant. Furthermore, the two years of data collection occurred in two droughty years which could have masked the beginnings of long term effects of season of defoliation on sward DMY and sward composition of *Festuca hallii.*

Festuca hallii made up 75% of the sward composition in October 1986, while in 1987 it had decreased ($P<0.05$) to 49% (Table

4.6). This would appear to be associated with the unusually high September 1986 precipitation (168% of normal) which resulted in a high *Festuca hallii* aboveground DMY in October of 1986 (Table 4.4, Figure 4.1). This indicates a sensitivity for *Festuca hallii* sward composition to timing of precipitation during the growing season.

The 1986-to-1987 decrease in the aboveground DMY for *Festuca hallii* in the October defoliation treatment is contrasted with an 88% and 38% increase in the aboveground DMY of the other grasses and grass-like species and forbs. This resulted in a 1986-to-1987 increase (P<0.05) in the sward composition for the other grasses and grass-like species of 10% to 24% for the October defoliation treatment. There was also an increase for the forbs in sward composition from 15% in 1986 to 26% in 1987 for the October defoliation treatment. The 1986-to-1987 contrasts may illustrate a relatively dramatic shift in sward composition in which October defoliation under drought conditions appears to favor the other grasses and grass-like species, and possibly the forbs, over *Festuca hallii*.

For *Festuca hallii* there was a significant year effect on sward composition with the 1987 decrease for *Festuca hallii* likely reflecting the drier growing season of 1987 compared to 1986. In contrast, the more xeric 1987 conditions may have favored the other grasses and grass-like species over *Festuca hallii* in terms of sward composition as there was no significant year effect on their sward composition or that of the forbs. This may reflect a greater persistence of production in the drier growing conditions of 1987 by the other grasses and grass-like species and the forb species compared to *Festuca hallii*.

Festuca hallii Responses - Morphological and Physiological

This study showed that the inflorescence density of *Festuca hallii* was affected ($P<0.01$) by the season of defoliation (Tables 4.7, 4.8, Figure 4.4). However, interpretation of the results is complicated by a significant defoliation-by-year interaction. The decline in inflorescence densities for the July and August treatments versus the increase for the September and October between 1986 and 1987 likely explains the defoliation treatment-by-year effect ($P<0.001$) when there was no significant year effect between 1986 and 1987.

Inflorescence densities for plants in the burnt control and August defoliation treatment were higher ($P<0.05$) than for plants in the June defoliation treatment in June 1986 (Table 4.8, Figure 4.4). The zero inflorescence count for the June defoliation treatment reflected the application of the 1986 June defoliation 14 days prior to sampling. This defoliation removed all inflorescences. The 1986 May defoliation treatment also removed inflorescences, thus contributing to that treatment's inflorescence density count of 1.7 m^{-2}. The 0.1 and 0.0 inflorescences m^{-2} for plants in the 1987 May and June defoliation treatments again reflected their partial or complete removal by the application of defoliation treatments shortly before the inflorescence density data were collected.

The purpose of this experiment was to investigate the effect of intense single annual defoliations at monthly intervals over the growing season on *Festuca hallii.* Therefore, the May and June results were a true reflection of the effect of season of defoliation on inflorescence density of *Festuca hallii* when the data were collected across all treatments at a single time in late June. Bailey and Anderson (1978) noted a similar reduction in *Festuca hallii* inflorescence density from a May 1971 defoliation by fire (1 m^{-2}) compared to an October 1970 defoliation by fire (35 m^{-2}), when the inflorescence data were counted in July, 1971. In contrast, work by Sinton (1980) found that in the growing season following defoliation, July and October defoliations significantly suppressed inflorescence production compared to high densities for plants defoliated in April and May. However, Sinton's (1980) work was based on only one year's data which would not allow for the year-to-year variability in the inflorescence production of *Festuca hallii* as demonstrated by the control in this study.

In southwestern Alberta, floral initiation for *Festuca campestris* is erratic. Johnston and MacDonald (1967) showed that partial floral initiation occurred between August and September in the year prior to bolting. Floral initiation for *Festuca hallii* is also erratic as shown by inflorescence densities changing 25 fold for the undisturbed control plants between 1986 and 1987 in this study (Table 4.8, Figure 4.4) and by Bailey and Anderson (1978). Given the close relationship between *Festuca hallii* and *Festuca campestris* (Pavlick and Looman, 1984), it is reasonable to assume that floral initiation also occurs for this species in the late summer prior to the year of bolting.

For the July, August, September, and October defoliation treatments, the inflorescence counts were taken before the defoliation treatments were applied in 1986 and 1987. It is of interest to note that in 1987 plants in the July and August treatments produced low numbers of inflorescences compared with plants in the other treatments for that year. There was a trend over both years for plants in the September and October defoliation treatments to have substantially higher inflorescence densities than plants in the May, June and July defoliation treatments.

Bailey and Anderson (1978) reported no difference between the nonburnt control and the October defoliation for inflorescence density of *Festuca hallii*. Similar results were obtained in this study (Table 4.8, Figure 4.4). This suggested that defoliation late in the season (September or October) is no different from the nonburnt control in terms of effects on inflorescence production in the following growing season. This would likely result from apices that were initiated prior to September (Johnston and MacDonald 1967), being unaffected by an October defoliation.

Willms et al. (1986) reported that removal of litter had no significant effect on *Festuca hallii* inflorescence production at Kinsella. Their study, however, reported only on inflorescence data for 1981 and with a control density of 8 m^{-2} compared to 34 m^{-2} in 1971 (Bailey and Anderson, 1978), and 48 m^{-2} in 1987 in this study.

This indicated that 1981 was a year of low inflorescence production. Therefore, the lack of inflorescence density response to litter removal reported by Willms et al. (1986) must to be taken with caution. In this study, partial litter removal in the burnt control and mowing in the September and October defoliation treatments appeared to enhance inflorescence production over both years, independent of the significant increase in the number of inflorescences for the control in 1987 over 1986. This increase in inflorescence density for the control was not likely caused by any alteration of the litter structure caused by sampling procedures because the location of the sample sites within the plots was randomly selected each year.

In summary, based on two years of data, a single May 1985 burn or the same burn with a 1986 and 1987 annual intense September or October defoliation, resulted in *Festuca hallii* producing the greatest number of inflorescences in 1986 and 1987, independent of the significant increase in the number of inflorescences for the control in 1987 over 1986. The lowest number of inflorescences were consistently produced by the intense annual May, June, and July defoliations. The results for annual August defoliation treatment were inconclusive.

Defoliation has been shown to increase tiller density of *Festuca campestris*, *Festuca hallii*, *Lolium multiflorum*,and *Lolium perenne* (Degregibus et al. 1983, Willms et al. 1986, Willms 1988). Increased tiller density in *Festuca campestris* was associated with an increase in phostosynthetically active radiation reaching the plant's crown following defoliation (Willms 1988). However, light quality may be more important than light intensity in the promotion of tillering. Increased tiller densities for both *Lolium* species was achieved when the stem bases of plants were exposed to light rich in red wavelenths versus light with only far-red wavelengths (Degregibus et al. 1983). Both the intensity and the richness of the red wavelenths in the light reaching the stem bases of *Festuca hallii* would have been increased following defoliation. This may explain the higher tiller densities for the burnt control and the season of defoliation treatments when compared to the control, with the exception of the June defoliation treatment (Figure 4.5, Table 4.10).

In this study, tiller density of *Festuca hallii* was affected ($P<0.001$) by the season of defoliation but there was no ($P>0.05$) year-to-year effect or season of defoliation-by-year interaction (Table 4.9). The most striking aspect of the season of defoliation results was the May-to-June-to-July contrasts in tiller density. Tiller density was negatively affected by late spring (early June) defoliation (Figure 4.5, Table 4.10). Clearly in terms of tiller density, *Festuca hallii* was most vulnerable to defoliation for a short interval before and after the early part of June. This vulnerability seemed to disappear by the beginning of July when plants had entered the ripe seed growth stage (Chapter III). The highest mean tiller density was achieved when plants were defoliated in October, although they did not produce any more tillers than when defoliated in July at a ripe seed growth stage.

Tiller densities were greatest in this study when stem base TNC (%) peaked in early July and October as noted in the growth cycle study (Chapter III). The July period also coincided with the termination of rapid growth and phenological changes occurring from the end of April until mid June. Conversely, the lower tiller density numbers for August and September also coincided with a decrease in stem base TNC (%) during those months. These results suggest that in terms of greatest vigor and defoliation resistance, early July and early October would be the optimal seasons of defoliation for *Festuca hallii*. Menke and Trlica (1983) found that defoliations of mature plants caused less loss of vigor than defoliation during rapid growth.

McLean and Wikeem (1985) found that a June defoliation significantly lowered tiller numbers when compared with a May or September defoliation. Sinton (1980) showed that in the first growing season following single defoliation treatments, the tiller density for plants in the June defoliation treatment was significantly lower than for those in either early or late April defoliation treatments. It appears that during April, the tiller density of *Festuca hallii* was not as vulnerable to defoliation as it was during June, which may explain, in part, why the results for the Willms et al. (1986) study were not more conclusive. Sinton and Bailey (1980) found that the tiller density for a July defoliation and October defoliation was also 90% higher than for the June defoliation treatment for the first growing season following defoliation. These results were almost identical to the pattern found in this study following three years of consecutive treatments. Sinton (1980), however, found that the tiller density for plants in the April and June defoliation treatments, in the second growing season after the defoliation treatment, rebounded so there was no significant differences between them and the July and October defoliation treatments. In all studies, however, there was a trend for annual defoliations later in the season (July to October) to cause an increase in tiller densities versus defoliations involving the June period. For each of the studies conducted on *Festuca hallii* at Kinsella there was a trend for defoliation to result in increased tiller density over nondefoliated control plants, except when defoliation was conducted during early June.

This study showed that the significant increases in tiller density were for the annual defoliations during early July or October over the control and June defoliation (Figure 4.5). There was no apparent relationship between tiller density and DMY or sward composition for the season of defoliation treatments (Figures 4.2, 4.3). This would suggest a decrease in tiller weight from June-to-July and from September-to-October.

Total nonstructural carbohydrates (TNC) in forage grasses include reducing sugars, nonreducing sugars, fructans, and starch (White 1973). These substances appear to be the primary energy reserves utilized by grasses for growth and dormant season maintenance. The role and importance of stem base TNC reserves in the initiation of spring growth or regrowth following defoliation is currently under debate and would appear to vary from species to species (Richards and Caldwell 1985). Historically there has been an emphasis placed on appropriate grazing management for maintaining adequate stem base TNC reserves for species vigor and regrowth following defoliation (White 1973). More recent work has shown that the TNC storage in other organs (e.g. roots, upper stems, sheaths), the photosynthetic capacity, the physiological mechanism of resource allocation for individual species, and tillering potential are also important factors in determining the ability of species to overwinter and to tolerate defoliation (Caldwell et al. 1981). However, stem base TNC concentration remains an important technique for evaluating grass energy reserves. (Volenec 1986).

Analysis of variance for the end-of-season stem base TNC (%) data indicated a season of defoliation treatment effect ($P<0.05$), but no ($P<0.05$) differences among treatments for either year were separated with the Bonferroni technique (Tables 4.9, 4.11). This is not a statistical contradiction but the difference between looking at all contrasts with the analysis of variance versus a priori specified contrasts with the Bonferroni multiple means technique (T. Taerum, personal communication, January, 1989)

Therefore, the intense single annual season of defoliation treatments over three years appear to have had no significant effect on end-of-season stem base DM weight, end-of-season stem base TNC (%) or end-of-season stem base TNC pool. This would suggest that the annual intense style of defoliation used in this study did not jeopardize the end-of-season energy reserves regardless of the season of defoliation. It was not determined from this study if these season of defoliation treatments altered the TNC (%) growth cycle pattern as a function of Julian date.

There was a significant year effect for the end-of-season stem base TNC (%) with reserves being lower in 1987 than in 1986. This could be related to September 1986 being 1.9° C below the long term monthly temperature average, whereas September 1987 was 2.9° C above the long term monthly temperature average. The lower September 1986 temperatures would likely lead to more rapid winter hardening and therefore higher TNC (%) values for October 1986 compared with October 1987. George et al. (1989) showed a 5% year-to-year difference for October stem base TNC (%) for *Panicum virgatum* which they attributed to year-to-year weather differences. A second factor is that the stem base TNC (%) began to increase rapidly after the beginning of September (Chapter III). Therefore, if the 1987 sampling date had been postponed another week, it is conceivable, on the basis of the 1987 TNC (%) growth cycle upswing in October, that the end-of-season TNC values would have been closer to those of 1986. This implies that in future, using the same sampling date could be very important, as there may be rapid changes in the TNC (%) in October associated with the plant preparing for winter dormancy. Using the same sampling date or phenological stage would limit this source of variation and help to separate treatment and year-to-year weather effects from any autumn growth cycle variation due to even small differences in the sampling date.

Plants of *Festuca hallii* in the burnt control and September defoliation treatments were both significantly lower in TNC (%) in 1987 compared to 1986. The higher than normal September 1987 temperatures following the above average precipitation in August 1987 would have created optimal conditions for late summer growth. These conditions may have increased the late summer growth of the burnt control resulting in the significantly lower TNC (%) in 1987 compared to 1986. For the September defoliation treatment, the same environmental conditions combined with the stimulation of an early September defoliation may also have optimized late summer regrowth rates, lowering the 1987 TNC (%) compared to 1986.

Coupland and Johnson (1965) described the root growth habit of *Festuca hallii* in the black soil zone of Saskatchewan near Saskatoon. At that location they found a maximum root depth to 110 cm with a lateral spread ranging between 13 to 25 cm. When moisture was limiting enough to permit the entrance of Mixed Prairie species, the maximum root depth declined to 60 cm. Earlier work showed that 73% of the roots for *Festuca hallii*, on a DM basis, were in the top 15 cm of a 122 cm profile (Coupland and Brayshaw 1953).

A trend for the end-of-season root DM weights to increase with each month's delay in application of the defoliation treatment was suggested in 1987 (Figure 4.6). Given that these are perennial plants, it is possible that this was a trend which might have become a significant season of defoliation response if a fourth year of treatment had been applied. Alternatively it could also reflect the plant allocating more resources to root growth versus foliage in 1987 due to the drier growing conditions (Table 2.3).

Crider (1955) dramatically illustrated how grass root growth can be affected by defoliation. However, Richards (1984) clearly showed that the root growth response of a grass to defoliation was species-specific and has important implications for a species' resistance to defoliation. From this study it would appear that there was no significant season of defoliation effect on root growth to the 7.5 cm depth. This may suggest that this species is the type that gives priority to root growth over tiller production independent of season of defoliation, and that root growth was not severely reduced by the season of defoliation treatments used in this study.

In summary, this study strongly suggests that *Festuca hallii* is the type of grass which may be well suited to a high intensity low frequency type of grazing management system. With only single annual defoliations, these results suggest that the plant is surprisingly resilient to high intensity defoliation independent of the season of defoliation. The optimum periods for defoliation in terms of plant vigor as measured by tiller density appear to be in early July and early October while the most detrimental period appears to be early June. Managing for optimum seed production would require defoliation as late in the growing season as possible.

CONCLUSIONS

This study demonstrated that three years of single annual intense season of defoliation treatments had certain effects on *Festuca hallii* within a *Festuca-Stipa* grassland in central Alberta.

Total annual DMY was not affected by season of defoliation under moisture limited growing conditions. Under the comparatively dry growing conditions of this study, timing of growing season precipitation appeared to have greater impact on total annual DMY than the season of a single annual intense defoliation.

Festuca hallii DMY was more responsive to above average amounts of precipitation than the forb DMY throughout the growing season. This characteristic was especially pronounced in the late summer growing period during which *Festuca hallii* would appear to have a competitive advantage over all the other sward species in utilizing late season precipitation.

The other grasses and grass-like species were not moisture limited as there was no DMY response to fluctuations in precipitation.

Sward composition for *Festuca hallii* was affected somewhat by season of defoliation. The May defoliation treatment resulted in the highest sward composition but this was likely caused by the early start of *Festuca hallii*'s growth compared with other sward component species. There was a trend for plants in the June to October season of defoliation treatments to have a lower composition of *Festuca hallii* than in the May defoliation treatment, but the sward composition differences varied from year-to-year and were likely influenced by precipitation distribution patterns within a given growing season.

Festuca hallii inflorescence density was enhanced by progressively delaying the season of defoliation. The highest inflorescence densities were obtained when defoliation was delayed till early October.

Tiller density would appear to be the most sensitive indicator of season of defoliation stress. Early June was clearly the period of greatest season of defoliation stress, while early July and early October were the periods of least defoliation stress as measured by tiller density.

Season of defoliation effects had no significant effects on stem base weight (g m^{-2}), TNC (%), TNC pool (g m^{-2}) or root DM weight (g m^{-2}) to the 7.5 cm depth indicating that these parameters of plant growth and vigor were not adversely affected by single annual intense defoliations over a three year period.

These results suggest that the optimum range condition for this *Festuca-Stipa* grassland would be achieved by delaying defoliation till after the beginning of September. At this point in the growing season there would be no apparent effect on *Festuca hallii* DMY but inflorescence density and tiller density would both be maximized. This would enable *Festuca hallii* to optimize both its sexual and vegetative reproduction strategies while being utilized in a grazing system.

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V. SOME EFFECTS OF FREQUENCY OF DEFOLIATION ON PLAINS ROUGH FESCUE IN CENTRAL ALBERTA

INTRODUCTION

Continuous grazing is widely practiced throughout Alberta (Walton et al. 1981). During the 1980s an increased interest in rotational grazing systems as an alternate to continuous grazing has developed throughout western Canada. An important question in the development of any grazing system, but especially rotational grazing systems, is how frequency of defoliation will affect the overall productivity of a grassland and in particular its key species. A strategic objective in range management research should be to establish the optimum defoliation regime that will maintain long term productivity of the key species of a given grassland. Determining how frequently a native grassland may be grazed in a growing season without causing ecological retrogression and loss of range condition is an important step in establishing this objective.

Festuca hallii (Vasey) Piper [1] is the key species in the *Festuca-Stipa* grasslands of central Alberta (Pavlick and Looman 1984, Wroe et al. 1988). This native grassland has been shown to have forage production equal to, or better than, the forage production of introduced *Bromus inermis-Festuca rubra* grasslands in the absence of a legume (Bailey et al. 1980). Average daily gains for steers of 1.1 kg under light (8 AUM) June grazing and 0.8 kg under light (8 AUM) autumn grazing on *Festuca-Stipa* grassland has been shown over a 11-year grazing study by Bailey et al. (1988). Most of this weight gain performance was attributable to *Festuca hallii* which may contribute more than 70% of the forage dry matter yield from *Festuca-Stipa* grasslands of central Alberta.

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[1] Scientific nomenclature follows Moss (1983) except where a different authority is cited in the text.

There has been some confusion in both the taxonomy and nomenclature of the North American rough fescues (Pavlick and Looman 1984, Harms 1985). Historically, the key species in the *Festuca-Stipa* grasslands of the aspen parkland of central Alberta and the *Festuca-Danthonia* grasslands of the Rocky Mountain foothills of south-western Alberta, has been called *Festuca scabrella* (Moss 1983). The rough fescues of these two regions have been commonly distinguished as the plains rough fescue and foothills rough fescue, respectively. The species nomenclature for the North American rough fescues as proposed by Pavlick and Looman (1984) will be followed in this paper with the plains rough fescue identified as *Festuca hallii* (Vasey) Piper and the foothills rough fescue as *Festuca campestris* Rydb.. When literature cited refers to *Festuca scabrella*, an effort will be made to interpret that literature as *Festuca campestris* or *Festuca hallii* on the basis of the geographic distribution of taxa as presented by Pavlick and Looman (1984) and Harms (1985).

A number of workers have demonstrated that a frequency of defoliation which is too high has negative effects on different forage grasses. The precise response to frequency of defoliation may be influenced by defoliation intensity or height (Willms 1983). In general, reduction of dry matter yield with increasing frequency of defoliation has been demonstrated for *Festuca campestris* (Willms 1983), *Bromus willdenowii* (Bell and Ritchie 1989), *Avena strigosa* and *Lolium perenne* grown with and without *Medicago truncatula* (Lowe and Bowdler 1988). Biswell and Weaver (1933) demonstrated a reduction in root growth as well as forage yield with frequent defoliation on a number of species from the Tallgrass Prairie of Nebraska. Thaine (1954) demonstrated a reduction of root weight but not forage yield with increasing frequency of defoliation in a greenhouse study with *Elymus junceus*. Some, but not all, of the studies cited showed how other plant parameters such as tiller density and total nonstructural carbohydrates, were affected by frequency of defoliation.

The reciprocal to frequency of defoliation is the concept of duration of rest. The length or duration of a given rest should be a function of the purpose of the rest (Tainton 1971). In North American range management terminology, rest implies absence of defoliation for a full growing season or during a critical portion of the plant development (Society for Range Management 1989). The Society for Range Management (1989) defined deferment as referring to a delay of defoliation for an adequate period of time to provide for plant reproduction, establishment of new plants, or restoration of vigor of existing plants. Holecheck et al. (1989) distinguishes rest from deferment as meaning that the grassland receives no use for a full year versus no grazing during the growth period portion of a year. In South African grassland terminology, a number of types of rest are distinguished depending upon the objectives that wish to be obtained by resting (Tainton 1971). These objectives involve an initial determination of whether the requirements of the animals or the plants are to have priority. When giving plants priority, Tainton (1971) distinguishes the following types of rests: period of absence or withdrawal, herbage accumulation rests, seeding rests, seedling establishment rests, vigor rests, tillering rests. The duration of each type of rest is a function both of the rest's purpose and the growth characteristics of the key species being managed for in a given sward.

This study focused on the notion of the vigor rest, as proposed by Tainton (1971). This type of rest emphasizes: (1) the establishment of pre-defoliation reserve levels to enable adequate recovery following defoliation, (2) the accumulation of reserves for periods of stress associated with defoliation, and (3) the promotion of a large assimilatory system to promote optimum forage production. It was important to determine what rest interval between intense defoliations is required for *Festuca hallii* in central Alberta in order to allow for its optimum production and vigor. In addition, this study sought to determine how frequency of defoliation affected sward composition and range condition of a *Festuca-Stipa* grassland, and the productivity and vigor of *Festuca* *hallii*. The study was a three-year (1985-1987) simulation of frequency of grazing effects on an undisturbed *Festuca-Stipa* grassland in central Alberta.

The specific purposes of this study were two-fold. The first purpose was to evaluate the effects of frequency of defoliation on the aboveground dry matter yield (DMY) and sward composition (DM%) of a *Festuca-Stipa* grassland. The second purpose was to evaluate the specific effects of frequency of defoliation on the inflorescence density, tiller density, and the end-of-season: stem base DM weight, stem base total nonstructural carbohydrates (TNC) percentage, stem base TNC pool and root DM weight of the key species, *Festuca hallii*.

MATERIALS AND METHODS

Study Area and Experimental Design

This study was a three year simulation of frequency of grazing effects using four treatments: 1, 2, 4, and 8-cuts per growing season. Intense defoliations (3 cm cutting height) were applied with a rotary mower to generate the 1-cut (mid-August), 2-cut (late June, mid-August), 4-cut (late May, late June, mid-July, mid-August) and 8-cut (every second week from mid-May to mid-August) defoliation treatments. They were repeated annually from 1985 to 1987.

The study area (53 °N latitude and 112 °W longitude) was located on Section 28 of the University of Alberta's research ranch approximately 150 km southeast of Edmonton, Alberta. The climate is a cold-temperate Boreal climate (Walter 1985) with an average annual temperature of 2° C and a total average annual precipitation of 432 mm, of which 323 mm or 75% falls mostly as rain between April and September. Elevation is approximately 700 m above sea level. The grassland soils are predominantly thin Orthic Black Chernozems (Howitt 1988). The grazing season is traditionally from May to December depending on the species being grazed and year-to-year differences in precipitation and snow cover.

The study area is on the northern edge of the grassland ecoclimatic province in Canada. It is a transitional zone between the more arid prairie to the south and the moister boreal forest to the north (Ecoregions Working Group 1989). Undisturbed areas are characterized by a mosaic of *Populus tremuloides* groves and *Festuca hallii* grasslands. Groves of trees occur on the moister sites with shrub and grassland communities on the drier sites. Shrub communities are dominated by *Amelanchier alnifolia*, *Elaeagnus commutata*, *Rosa acicularis*, *Rosa woodsii* and *Symphoricarpos occidentalis*. *Festuca hallii* dominates open undisturbed sites but *Stipa curtiseta* co-dominates on grazed sites (Wheeler 1976). Recent research indicates that *Festuca hallii* is also the dominant in autumn grazed areas (Bailey et. al 1988). Other grasses characteristic of the area depending on site, aspect, moisture and disturbance include; *Agropyron smithii*, *Agropyron trachycaulum*, *Agrostis scabra*, *Bouteloua gracilis*, *Festuca saximontana*, *Koeleria macrantha*, *Helictotrichon hookeri* and *Poa* *pratensis*. *Artemisia frigida* was a characteristic woody increaser on disturbed sites.

The specific study site was a 22.5 ha wedge of the aspen parkland mosaic consisting of grassland (3.4 ha or 21%) and aspen forest and shrubs (17.8 ha or 79%) running north south on the east side of Carrier Lake. This site was located within the boundaries of the University of Alberta Ranch, and had not been grazed for about 25 years. At the beginning of May, 1985, ten blocks within the grassland area were burned to remove the heavy accumulation of litter. Control plots (2 X 10 m) adjacent to each burned block were established. Within each block, randomized plots (2 X 10 m) for a burnt control, and 1, 2, 4, and 8-cut frequency of defoliation treatments were established. One side of each treatment plot was randomly selected for mowing of the yield strip. The opposite side of each treatment plot was used for placement of sampling quadrats. The entire 2 X 10 m treatment plot was defoliated each time a treatment was applied.

Sward Dry Matter Yield

For each defoliation treatment the aboveground dry matter yield (DMY) was measured by collecting the sample material which was cut from a 600 cm by 52 cm strip at a height of 3 cm with an Arien 21" self-propelled rotary mower (McGinnies 1959). The sample material from these mowed plots were placed in paper bags, air dried, and sifted with a 4.8 mm (6/32") rice sieve to remove any litter and soil mixed with the forage sample. The sifted samples were oven-dried at 65° C to a constant weight to determine aboveground DMY. Dry matter yields of *Festuca hallii*, other grasses and grass-like species, forbs, and woody species were estimated based on their sward composition (DM%) for each treatment plot. The frequency of defoliation treatment and sampling schedule is summarized in Table 5.1.

Sward composition

At the midpoint of the frequency of defoliation schedule in 1986 and 1987, prior to the first cut of the 2-cut frequency of defoliation treatment, the control, burnt control, 1, 2, 4, and 8-cut frequency of defoliation treatments were sampled for sward composition (Table 5.1). Samples were taken from two randomly located 0.25-m ^{2} quadrats placed on the side opposite to that used for the yield strip within each treatment plot. These quadrats were permanent for the 1, 2, 4, and 8-cut frequency of defoliation treatments. The quadrats were randomly selected in both 1986 and 1987 in the control and burnt control in order to sample previously unharvested vegetation.

The aboveground biomass was hand-clipped and separated into *Festuca hallii*, other grasses and grass-like species, forbs, and woody components. The litter component was hand-raked from each plot prior to the hand-clipping. Each component was oven-dried at 65° C to a constant weight. Sward composition was calculated based

Table 5.1 Dates of the 1, 2, 4, and 8-cut frequency of defoliation treatments and date of collection of sward composition, inflorescence density, tiller density, and stem base core samples for 1985, 1986, and 1987.

			Date of sampling					
			May	Jun	Jul	Aug	Sep	Oct
1985	Defoliations [1]	1-cut				24		
		2-cut		28		24		
		4-cut		3, 28	24	24		
		8-cut	17	3,13,28	11, 24	7, 24		
1986	Defoliations	1-cut				19		
		2-cut		26		19		
		4-cut	26	26	23	19		
		8-cut	13, 26	10, 26	8, 23	7, 19		
	Sward composition [2]			23-25				
	Inflorescence density [2]			18				
	Tiller density [2]			18-20				
	Stem base cores [2]							10
1987	Defoliations	1-cut				24		
		2-cut			5	24		
		4-cut		3	5, 28	24		
		8-cut	22	3, 17	5,15,28	12, 24		
	Sward composition [2]			29-30				
	Inflorescence density [2]			22-23				
	Tiller density [2]			22-24				
	Stem base cores [2]							2-3

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[1] On May 3, 1985 defoliation occurred by burning of all plots during clearing of block areas. See Figure 2.1 for further detail.

[2] All plots sampled on dates indicated.

on the relative dry matter weight of the living (green) components after deducting the litter component. The relative percentage of the living components was used to calculate the DMY of *Festuca hallii*, other grasses and sedges, forbs, and woody species for the control, burnt control and each frequency of defoliation treatment plot.

Inflorescence Density

Festuca hallii inflorescence density was determined on June 18, 1986 and between June 22 & 23, 1987 by counting the inflorescences in two randomly located 0.5-m ^{2} quadrats placed on the opposite side to the yield strip within each treatment plot. These quadrats were permanent for each of the 1, 2, 4, and 8-cut frequency of defoliation treatments. The quadrats were randomly selected in both 1986 and 1987 in the control and burnt control to sample previously unharvested vegetation in both years.

Tiller Density

Festuca hallii tiller density was determined in 4 randomly located 0.04-m ^{2} quadrats placed on the opposite side to the yield strip within each treatment. The 0.04-m ^{2} quadrat size was determined by using the Two-Term Local-Quadrat Variance (TTLQV) method in order to minimize sampling variance (Ludwig, 1979). These quadrats were permanently located in the 1, 2, 4, and 8-cut frequency of defoliation treatments. The quadrats were randomly selected in both 1986 and 1987 in the control and burnt control so that previously unharvested vegetation would be sampled in each year.

End-of-season Stem Base Weight, TNC (%), TNC Pool, and Root Weight

Festuca hallii stem base weight, total nonstructural carbohydrate percentage (TNC (%)), and TNC pool were determined by removing four 7.0 cm diameter by 7.5 cm deep cores from each treatment on October 10, 1986 and October 2-3, 1987. The cores were immediately placed in plastic bags, sealed, transported to a freezer, and frozen within thirty-six hours of extraction from the ground. Prior to analysis, the samples were thawed overnight at room temperature. The foliage was trimmed to 2 cm above the soil surface. The cores were separated and washed under cool tap water over a 2 mm screen to remove soil from the roots. During the washing process, the non-*Festuca hallii* species were separated and discarded. The *Festuca hallii* stem bases and roots were separated by trimming 2 to 4 mm below the interface of the stem base and roots. Rhizomes were retained with the stem bases. The stem base and root samples were oven-dried at 65° C to a constant weight and weighed. The stem base samples were ground using a Udy cyclone mill (1-mm screen). The ground stem base samples were frozen until later analysis. The root samples were weighed and discarded.

Prior to TNC analysis, the stem base samples were removed from the freezer and dried overnight to a constant weight at 65° C and then stored in a desiccator. Stem base TNC (%) was determined with an acid hydrolysis technique adapted from Smith (1981) in consultation with M. J. Trlica, (personal communication, February 1987) and J. H. Richards (personal communication, May 1987). Duplicate 100-mg samples were refluxed for each treatment in 6 ml of 0.2N H_2SO_4 for 1 hour in a marble capped 25 X 200 mm test tube enclosed in a boiling water bath. The amount of TNC in each sample was determined by the Schaeffer Somogyi copper-iodometric titration technique as outlined by Smith (1981).

The stem base TNC pool was determined by multiplying the stem base weight by the TNC (%) to provide an estimate of the TNC pool (g m^{-2}).

Statistical Analysis

Data were analyzed by analysis of variance. Analysis of aboveground DMY was limited to the 1, 2, 4, and 8-cut frequency of defoliation treatments. Analyses for all other parameters included the control and burnt control treatments as well as the four frequency of defoliation treatments. Multiple comparisons were made using Bonferroni's method which determined significant differences simultaneously between treatments within a year and between years for a treatment (Milliken and Johnson 1984, T. Taerum, personal communication, January 1989). When there was no significant year or frequency of defoliation-by-year interaction, the averaged treatment results for the two years were analyzed with a one-way analysis of variance and the treatment means were separated using Student-Newman-Keuls multiple means test to determine significant differences. Percentage data were analyzed with and without a Box-Cox transformation (Sokal and Rohlf 1981). Both transformed and untransformed data sets gave the same significant analysis of variance and multiple means separation.

RESULTS

Sward Dry Matter Yield

Total aboveground dry matter yield (DMY) was determined for the sward as a whole, and for the sward components of *Festuca hallii*, other grasses and grass-like species, forbs, and woody species for the 1, 2, 4, and 8-cut defoliation treatments (Tables 5.2, 5.3).

The total sward DMY had a frequency of defoliation-by-year interaction ($P<0.001$), a year-to-year effect ($P<0.001$), and a frequency of defoliation response ($P<0.001$) (Table 5.2).

The total sward DMY treatment average of 193 g m^{-2} in 1986 was higher ($P<0.001$) than the 126 g m^{-2} for 1987 (Table 5.2). This year-to-year effect was likely associated with differences in the year-to-year accumulated precipitation to the end of July, which in 1986 was 262.2 mm (92% of normal), and for 1987 was 206.5 mm (72% of normal) (Table 2.3). The 21% reduction in accumulated precipitation to the end of July in 1987 compared to 1986 would have contributed to the 1986-to-1987 total sward DMY reduction

Table 5.2 Mean square values of aboveground dry matter yield for the total sward, *Festuca hallii,* other grasses and grasslike species, forbs, and woody species in the 1, 2, 4, and 8-cut defoliation treatments for 1986 and 1987.

Source	df	Total sward	*Festuca hallii*	Other grasses and grasslike species	Forbs	Woody species
Block (B)	9	2478 *	3405 *	859	6919 ***	19.9
Defoliation (D)	3	20997 ***	13860 ***	497	3046	7.7
Error 1 (B x D)	27	960	1283	654	1115	8.9
Years (Y)	1	92065 ***	27491 ***	5882 **	3363 *	7.1 *
Error 2 (B x Y)	9	382	879	267	414	1.2
D X Y	3	2085 ***	1364 *	418	536 *	2.5
Error 3 (B x D x Y)	27	222	428	150	154	1.8

*, **, and *** indicate significant variances for $P<0.05$, 0.01, and 0.001, respectively.

(P<0.05) for each frequency of defoliation treatment (Table 5.3, Figure 5.1).

Timing of precipitation during the growing season would have also contributed to the year-to-year differences (P<0.001), and to the frequency of defoliation-by-year interaction (P<0.001) for total sward DMY (Tables 2.2, 2.3, 5.2). The accumulated precipitation to the end of May was about the same for both years with 86.3 mm (71% of normal) in 1986, and 88.8 mm (74% of normal) in 1987. The major 1986-to-1987 precipitation timing differences were 60.4 mm (78% of normal) in contrast to 33.8 mm (43% of normal) for June, and 115.5 mm (134% of normal) in contrast to 83.9 mm (97% of normal) for July.

The total sward DMY for the 8-cut defoliation treatments was lower (P<0.05) than the 1-cut and 2-cut frequency of defoliation treatments in both years (Table 5.3, Figure 5.1). This would have contributed to the strong frequency of defoliation effect (P<0.001), despite the influence of the frequency of defoliation-by-year interaction (P<0.001) (Table 5.2).

Within years, the 1986 1-cut and 2-cut defoliation treatment had a higher (P<0.05) total sward DMY than the 4-cut and 8-cut defoliation treatments (Table 5.3, Figure 5.1). There was a stairstep decrease in DMY with increasing frequency of defoliation in 1986. The stairstep effect disappeared in 1987 with no (P>0.05) differences among the total sward DM yields for the 1, 2, and 4-cut

Table 5.3 Aboveground dry matter yield (DMY) of total sward, *Festuca hallii*, grasses and grass-like species, forbs, and woody species in the 1, 2, 4, and 8-cut defoliation treatments, with percentage change of DMY in the 2, 4, and 8-cut defoliation treatments over that in the 1-cut treatment, for 1986 and 1987.

Vegetation Type	Defoliation treatment	Total dry matter yield ----(g.m^{-2})----		% change over 1-cut -----(%)-----	
		1986	1987	1986	1987
Total sward	1-cut	231 a*	136 a*	100	100
	2-cut	221 a*	149 a*	96	112
	4-cut	178 b*	129 ab*	77	97
	8-cut	145 b*	87 b*	63	65
Festuca hallii	1-cut	131 a*	72 a*	100	100
	2-cut	111 ab*	76 a*	85	106
	4-cut	78 bc	58 ab	59	81
	8-cut	60 c*	26 b*	46	37
Other grasses & grass-like species	1-cut	49 a*	22 a*	100	100
	2-cut	34 a	21 a	70	93
	4-cut	30 a	24 a	62	107
	8-cut	47 a*	25 a*	97	111
Forbs	1-cut	49 ab	41 a	100	100
	2-cut	75 a*	52 a*	155	129
	4-cut	67 ab	47 a	138	115
	8-cut	37 b	36 a	75	88
Woody species	1-cut	2.2 a	1.6 a	100	100
	2-cut	1.2 a	0.4 a	54	27
	4-cut	2.3 a	0.9 a	108	57
	8-cut	0.5 a	0.8 a	21	48

The same letter following means within columns and vegetation group indicates no significant difference (Bonferroni; $P<0.05$).

An * indicates a significant difference between years for that treatment (Bonferroni; $P<0.05$).

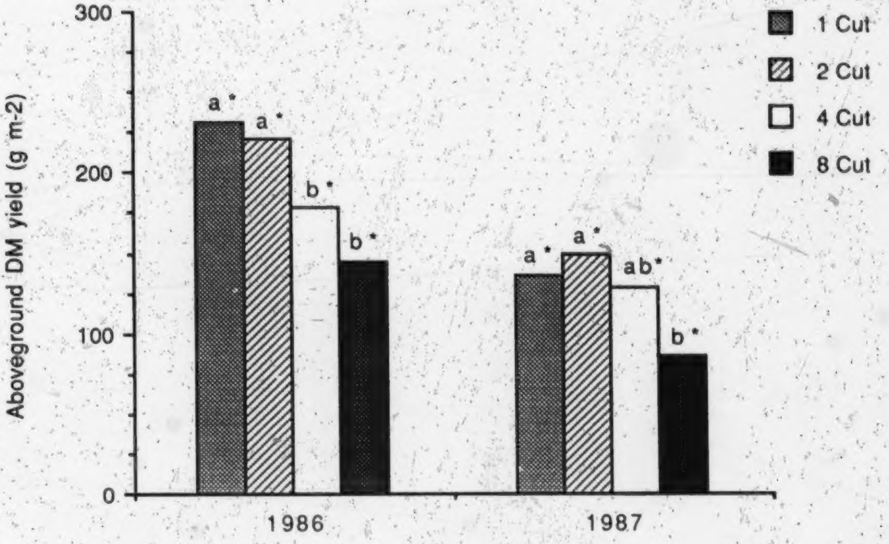

Figure 5.1 Aboveground dry matter (DM) yield of the sward by frequency of defoliation treatment for 1986 and 1987. Different letters above a bar indicate significant treatment differences within a year (Bonferroni; P<0.05). An * indicates a significant difference between years for that treatment (Bonferroni; P<0.05).

defoliation treatments. The lack of difference ($P>0.05$) between these frequency of defoliation treatments in 1987 may have reflected the influence of the 1987 June precipitation which was only 33.8 mm (43% of normal). The year-to-year differences in total sward DM yields with increasing frequency of defoliation would have contributed to the strong frequency of defoliation-by-year interaction ($P<0.001$) (Table 5.2).

The *Festuca hallii* DMY also had a frequency of defoliation-by-year interaction ($P<0.05$), a year-to-year effect ($P<0.001$), and a frequency of defoliation response ($P<0.001$) (Table 5.2).

The overall *Festuca hallii* DMY treatment average of 95 g m^{-2} in 1986 was higher ($P<0.001$) than the 58 g m^{-2} for 1987 (Table 5.2). There was no difference ($P>0.05$) between 1986 and 1987 for the *Festuca hallii* DM yields from the 4-cut treatment (Table 5.3, Figure 5.2). However, the *Festuca hallii* DM yields for the 1, 2, and 8-cut treatments were higher ($P<0.05$) in 1986 than in 1987. These year-to-year differences in results were again likely associated with the effect of the year-to-year differences in accumulated precipitation to the end of July (Table 2.3). Timing of precipitation during the growing season would have also contributed to the year-to-year differences ($P<0.001$), and to the frequency of defoliation-by-year interaction ($P<0.001$), for *Festuca hallii* DM yields (Tables 2.2).

The strong year ($P<0.001$) effect is also reflected in the reduced foliage regrowth of *Festuca hallii* for every cut in all

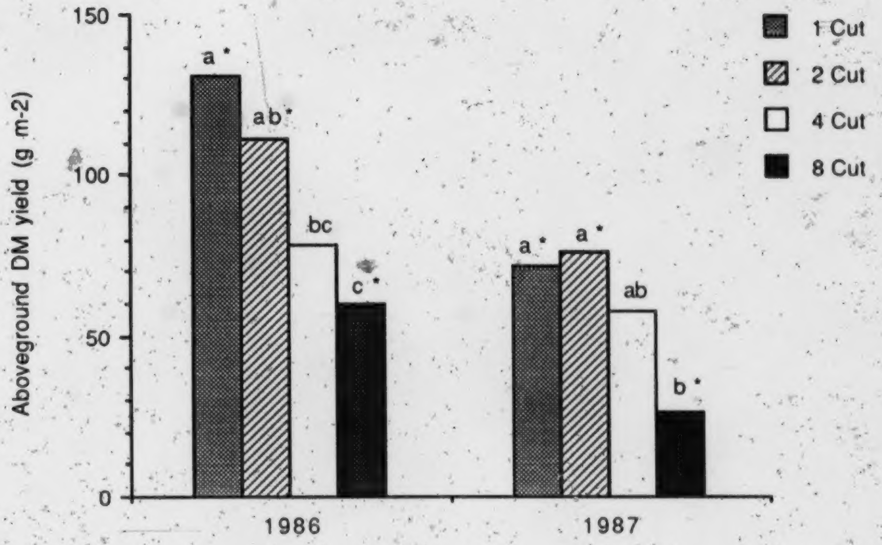

Figure 5.2 Aboveground dry matter (DM) yield of *Festuca hallii* by defoliation treatment for 1986 and 1987. Different letters above bars indicate significant treatment differences within a year (Bonferroni; $P<0.05$). An * indicates a significant difference between years for that treatment (Bonferroni; $P<0.05$).

treatments in 1987 compared with 1986, with the exception of the first cut of the 4-cut defoliation treatment (Table 5.4). There was a marked reduction in foliage regrowth after the 2nd cut of the 4-cut and the 4th cut of the 8-cut treatments, respectively, in 1986 (Figures 5.3, 5.4). This reduction coincided with the end of June. For both the 4-cut and 8-cut treatments in 1987, regrowth yields from the *Festuca hallii* plants after the first cut were drastically reduced, with regrowth yields for the subsequent cuts ranging from 19% to 76% of the corresponding cut in 1986. The individual 4-cut and 8-cut treatment cuts which had the lowest regrowth DM yields of *Festuca hallii* in 1987 compared to 1986, were from the beginning of June to the beginning of July. The 1987 regrowth yields of these cuts ranged between 19% and 41% of the 1986 yields. This period was preceded by precipitation in May and June of 24.8 mm (55% of normal) and 33.8 mm (43% of normal) in 1987. The major separation of the year-to-year differences in accumulated foliage regrowth of *Festuca hallii* for both the 4-cut and 8-cut treatments occurred from late May to early July.

The *Festuca hallii* DM yields for the 8-cut defoliation treatments were lower ($P<0.05$) than the 1-cut and 2-cut frequency of defoliation treatments in both years (Table 5.3, Figure 5.2). This would have contributed to the strong frequency of defoliation effect ($P<0.001$), despite the influence of the frequency of defoliation-by-year interaction ($P<0.05$) (Table 5.2).

Table 5.4 Dry matter yield of *Festuca hallii* foliage regrowth by defoliation cut number and treatment total in the 1, 2, 4, and 8-cut defoliation treatments for 1986 and 1987.

		----1986----		----1987----		87/86
Treatment	Cut #	Date	g m^{-2}	Date	g m^{-2}	%
1-Cut	1	19 Aug	131	24 Aug	72	55
		Total	131	Total	72	55
2-Cut	1	26 Jun	66	5 Jul	48	73
	2	19 Aug	45	24 Aug	28	62
		Total	111	Total	76	69
4-Cut	1	26 May	30	3 Jun	30	100
	2	26 Jun	24	5 Jul	10	41
	3	23 Jul	13	28 Jul	10	76
	4	19 Aug	11	24 Aug	8	74
		Total	78	Total	58	75
8-Cut	1	13 May	14	22 May	10	70
	2	26 May	13	3 Jun	4	33
	3	10 Jun	11	17 Jun	2	19
	4	26 Jun	7	5 Jul	2	31
	5	8 Jul	4	15 Jul	2	43
	6	23 Jul	5	28 Jul	2	51
	7	7 Aug	3	12 Aug	2	62
	8	19 Aug	3	24 Aug	2	61
		Total	60	Total	26	44

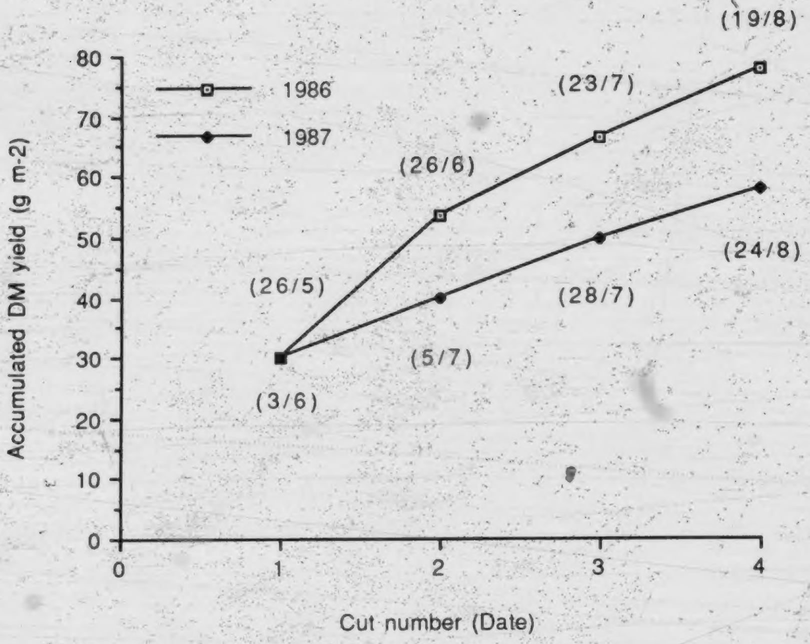

Figure 5.3 Accumulated dry matter (DM) yield of *Festuca hallii* foliage regrowth by cut number for the 4-cut defoliation treatment for 1986 and 1987.

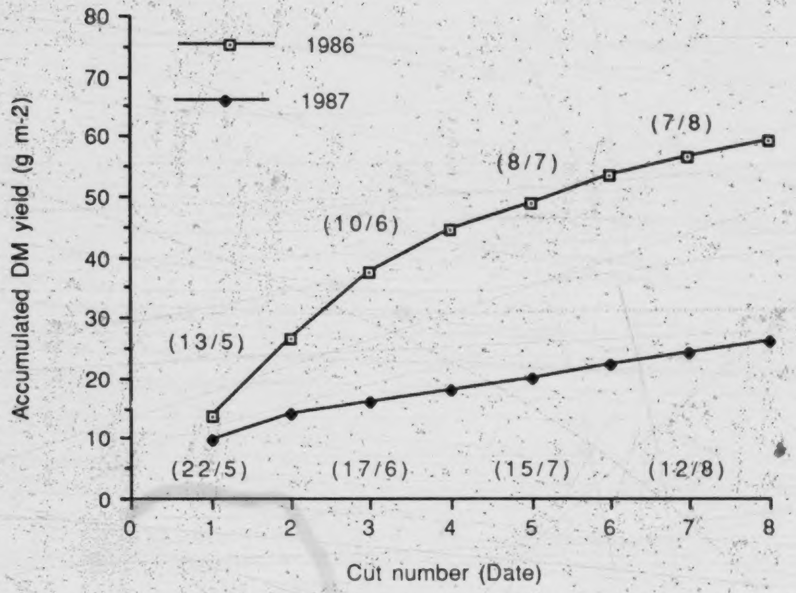

Figure 5.4 Accumulated dry matter (DM) yield of *Festuca hallii* foliage regrowth by cut number for the 8-cut defoliation treatment for 1986 and 1987.

The 1-cut defoliation treatment had a higher ($P<0.05$) *Festuca hallii* DMY than the 4-cut and 8-cut defoliation treatments in 1986 (Table 5.3, Figure 5.2). The stairstep decrease for DMY in 1986 was likely associated with increasing frequency of defoliation. The stairstep effect also disappeared for *Festuca hallii* in 1987, with no ($P>0.05$) differences among DM yields for the 1, 2, and 4-cut defoliation treatments. The lack of difference ($P>0.05$) between these frequency of defoliation treatments in 1987 likely reflected again the influence of the low June precipitation in 1987. These year-to-year differences in *Festuca hallii* DM yields in response to increasing frequency of defoliation would have contributed to the frequency of defoliation-by-year interaction ($P<0.05$) (Table 5.2).

The other grasses and grass-like species DMY had a year-to-year effect ($P<0.01$), but no frequency of defoliation-by-year interaction ($P>0.05$), nor frequency of defoliation response ($P>0.05$) (Table 5.2). The overall other grasses and grass-like species DMY treatment average of 40 g m^{-2} in 1986 was higher ($P<0.001$) than the 23 g m^{-2} for 1987 (Table 5.2). There was no difference ($P>0.05$) between 1986 and 1987 for the other grasses and grass-like species DM yields from the 2-cut and 4-cut treatments (Table 5.3). The other grasses and grass-like species DM yields for the 1-cut and 8-cut treatments were higher ($P<0.05$) in 1986 than in 1987, however.

The forb DMY had a year-to-year effect ($P<0.05$) and a frequency of defoliation-by-year interaction ($P<0.05$), but no frequency of defoliation response ($P>0.05$) (Table 5.2).

The overall forb DMY treatment average of 57 g m^{-2} in 1986 was higher ($P<0.001$) than the 44 g m^{-2} for 1987 (Table 5.2). There was no difference ($P>0.05$) between 1986 and 1987 for the forb DM yields from the 1, 4, and 8-cut treatments (Table 5.3). The forb DMY for the 2-cut treatment was higher ($P<0.05$) in 1986 than in 1987. This would correspond with the 1986 forb regrowth of the 2-cut treatment occurring during July which had 115.5 mm of precipitation (134% of normal) (Table 2.3). The above normal precipitation for July would have also contributed to the higher ($P<0.05$) forb DMY for the 2-cut treatment compared to the 8-cut treatment in 1986. These year-to-year differences in the response of the forb DMY to the frequency of defoliation treatments would contribute to the frequency of defoliation-by-year interaction ($P<0.05$) (Table 5.2).

Analysis of variance for DMY of the woody species indicated a year-to-year effect ($P<0.05$), but no frequency of defoliation-by-year interaction ($P>0.05$) nor frequency of defoliation response ($P>0.05$) (Table 5.2). The overall woody species DMY treatment average of 1.5 g m^{-2} in 1986 was higher ($P<0.05$) than the 0.9 g m^{-2} for 1987. The reliability of the results for the woody species must be taken with caution, however, as there was inadequate homogeneity of variance for a proper analysis of variance for the DM yields.

Sward Composition

Sward composition on a dry matter percentage basis (DM%) was estimated for the sward components of *Festuca hallii*, other grasses and grass-like species, forbs and woody species for the control, burnt control, 1, 2, 4, and 8-cut treatments.

The *Festuca hallii* sward composition had a season of defoliation-by-year interaction ($P<0.05$) and a season of defoliation response ($P<0.001$), but no year-to-year effect ($P>0.05$) (Table 5.5).

The *Festuca hallii* sward composition decreased in a stepwise progression with increasing frequency of defoliation in 1986 (Table 5.6, Figure 5.5). The stepwise decrease in sward composition with increasing frequency of defoliation disappeared in 1987 as the sward composition for the burnt control was higher ($P<0.05$) than sward composition of the control, and the sward composition for the 1-cut and 2-cut treatments were virtually identical. Overall, however, there remained a progressive decrease for the *Festuca hallii* sward composition with increasing frequency of defoliation for both years. These year-to-year differences in sward composition responses for individual treatments would have contributed to the frequency of defoliation-by-year interaction ($P<0.05$) (Table 5.5).

In both 1986 and 1987 the *Festuca hallii* sward composition in the 4-cut and 8-cut treatments were lower ($P<0.05$) than the *Festuca hallii* sward composition in the control and burnt control

Table 5.5 Mean square values of sward composition for *Festuca hallii*, other grasses and grass-like species, forbs, and woody species in the 1, 2, 4, and 8-cut defoliation treatments for 1986 and 1987.

Source	df	*Festuca hallii*	Other grasses and grass-like species	Forbs	Woody species
Block (B)	9	2173 ***	298	2893 ***	25.1
Defoliation (D)	5	3345 ***	1701 *	845 *	53.2 *
Error 1 (BxD)	45	299	256	246	17.0
Years (Y)	1	59	65	324 *	4.7
Error 2 (BxY)	9	151	56	59	11.7
D X Y	5	212 *	49	280 *	8.4 *
Error 3 (BxDxY)	45	71	32	52	9.4

*, **, and *** indicate significant variances for $P<0.05$, 0.01, and 0.001, respectively.

Table 5.6 Sward composition of *Festuca hallii*, other grasses and grass-like species, forbs, and woody species in the control, burnt control, 1, 2, 4, and 8-cut defoliation treatments, with percentage change of sward composition in the control, burnt control, 2, 4, and 8-cut defoliation treatments over that in the 1-cut treatment, for 1986 and 1987.

		Sward composition (DM%)		Percentage (%) change over 1-cut	
Vegetation Type	Defoliation treatment	1986	1987	1986	1987
Festuca hallii	Control	70.1 a	64.4 b	123	121
	Burnt Cntrl	64.0 a	72.5 a	112	136
	1-cut	57.0 ab	53.2 bc	100	100
	2-cut	51.0 ab	53.1 bc	90	100
	4-cut	44.5 b	44.9 cd	78	84
	8-cut	40.0 b	29.8 d	70	56
Other grasses & sedges	Control	5.2 b	6.8 b	24	42
	Burnt Cntrl	8.4 b	8.6 b	39	53
	1-cut	21.4 ab	16.1 ab	100	100
	2-cut	15.8 b	14.3 ab	74	89
	4-cut	17.6 ab	19.1 ab	82	119
	8-cut	34.7 a	29.4 a	162	183
Forbs	Control	21.0 a	24.4 ab	101	83
	Burnt Cntrl	22.4 a	16.6 b	108	56
	1-cut	20.7 a	29.5 ab	100	100
	2-cut	32.6 a	32.3 ab	158	110
	4-cut	36.5 a	35.3 a	176	120
	8-cut	25.1 a*	40.0 a*	121	136
Woody	Control	3.7 a	4.4 a	411	400
	Burnt Cntrl	5.2 a	2.4 a	578	218
	1-cut	.9 a	1.1 a	100	100
	2-cut	.6 a	.3 a	67	27
	4-cut	1.4 a	.7 a	156	64
	8-cut	.3 a	.9 a	33	82

The same letter following means within columns and vegetation type indicates no significant difference (Bonferroni; $P<0.05$).
* Indicates a significant difference between years for that treatment (Bonferroni; $P<0.05$).

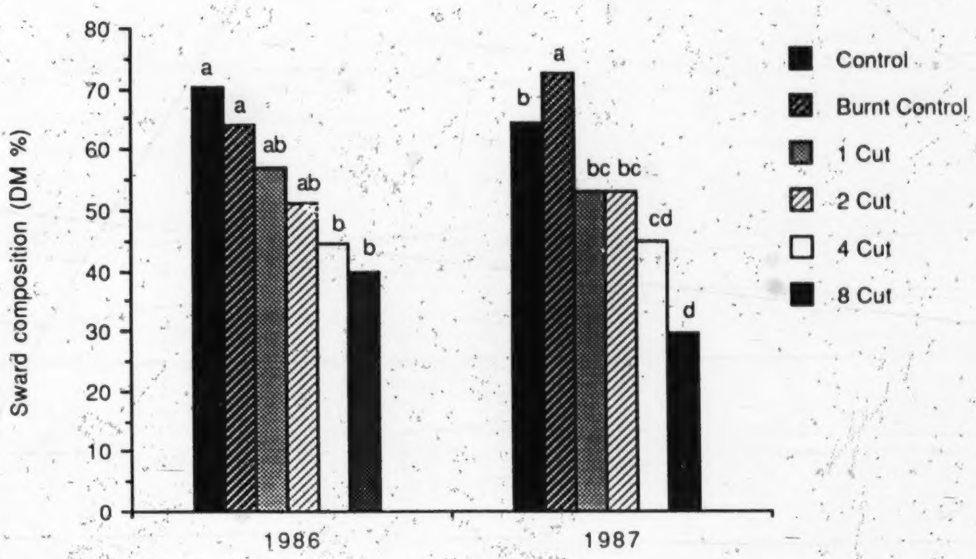

Figure 5.5 Sward composition of *Festuca hallii* by defoliation treatment for 1986 and 1987. Different letters above bars indicate significant treatment differences within a year (Bonferroni; P<0.05).

(Table 5.6, Figure 5.5). This year-to-year consistency of response for these treatments would contribute to the strong frequency of defoliation effect ($P<0.001$) for the sward composition of *Festuca hallii* (Table 5.5).

The other grass and grass-like species sward composition had a frequency of defoliation response ($P<0.05$) but no frequency of defoliation-by-year interaction ($P>0.05$) or year-to-year effect ($P>0.05$) (Table 5.5). Only the 8-cut defoliation treatment had a sward composition for the other grasses and grass-like species which was higher ($P<0.05$) than the sward composition for the control and burnt control in both years (Table 5.6). As there were no ($P>0.05$) differences between the DM yields among the frequency of defoliation treatments for the other grasses and grass-like species in either year, this increase in the sward composition of the other grasses and grass-like species would likely reflect corresponding decreases in the DM yields and sward composition of other sward components (Table 5.3).

The forb sward composition had a frequency of defoliation-by-year interaction ($P<0.05$), a season of defoliation response ($P<0.05$), and in contrast to the other sward components, a year-to-year effect ($P<0.05$) (Table 5.5).

The forb sward composition treatment average in 1986 of 26.4% was lower ($P<0.05$) than the 29.7% for 1987 (Table 5.5). This increase for the forbs' sward composition in 1987 was likely a function of the variable response of the different sward components to the year-to-year differences in growing conditions. Every sward component had a significant decrease in the overall treatment average for DMY for 1987 compared to 1986 (Table 5.2). The magnitude of the 1986-to-1987 DMY decreases was much larger for *Festuca hallii* (95 g m^{-2} to 58 g m^{-2}) and the other grasses and grass-like species (40 g m^{-2} to 23 g m^{-2}) than for the forbs (57 g m^{-2} to 44 g m^{-2}) or woody species (1.5 g m^{-2} to 0.9 g m^{-2}). The relative differences among these sward component DMY decreases would therefore have resulted in the overall treatment average for the forb sward composition increasing for 1987 compared to 1986, even though the forb DMY had also decreased in 1987 compared to 1986.

The forb sward composition was higher ($P<0.05$) in 1987 than in 1986 for the 8-cut defoliation treatment (Table 5.6). This year-to-year increase in sward composition of the forbs for the 8-cut frequency of defoliation treatment was likely related to the significant 1986-to-1987 reductions in the DM yields for *Festuca hallii* and the other grasses and grass-like species when there was no ($P>0.05$) 1986-to-1987 change in forb DMY (Table 5.3).

There were no ($P>0.05$) differences among the frequency of defoliation treatments for the forb sward composition in 1986 (Table 5.6). The forb sward composition for both the 4-cut and 8-cut treatments were higher ($P<0.05$) than the burnt control in 1987. The year-to-year difference in the forb sward composition responses to increasing frequency of defoliation would contribute to the frequency of defoliation-by-year interaction (Table 5.5). The frequency of defoliation response ($P<0.05$) was likely associated with increased forb sward composition as a function of increased frequency of defoliation, but the frequency of defoliation-by-year interaction makes the clarity of this response uncertain for this data.

The woody species sward composition had a frequency of defoliation-by-year interaction ($P<0.05$) and a frequency of defoliation response ($P<0.05$), but no year-to-year effect ($P>0.05$) (Table 5.5). The results for the woody species sward composition need to be taken with caution, however, given the small values that the woody species represent in the sward composition of the sward as a whole, and an inadequate homogeneity of variance for a reliable analysis of variance for the sward composition of the woody species.

Multiple means separation indicated no ($P>0.05$) differences among the frequency of defoliation treatments for sward composition of the woody species in either year (Table 5.6). These results did not reflect the visual observation of a clear increase in *Artemisia frigida* by 1987 for the 8-cut defoliation treatment. This increase occurred in patches of growth with a very low, flat, and very fine growth habit thereby avoiding the biweekly defoliation by the mower which the more upright growing grasses and forbs were not able to avoid. The visually observed increase of

Artemisia frigida in the 8-cut defoliation treatment indicated a decrease in range condition for that treatment (Wroe et al. 1988).

Inflorescence Density

The inflorescence density of *Festuca hallii* had a frequency of defoliation-by-year interaction ($P<0.01$), a year-to-year effect ($P<0.01$), and a frequency of defoliation response ($P<0.01$) (Table 5.7). The low inflorescence density values for the 4-cut and 8-cut defoliation treatments were largely due to the sampling dates being at the end of June, after the 1st cut of the 4-cut treatment, and the 3rd cut of the 8-cut treatment, had been applied (Table 5.1). Therefore these treatments were not included in the statistical analysis but their values were recorded (Table 5.8, Figure 5.6).

The *Festuca hallii* inflorescence density treatment average in 1986 of 13 m^{-2} was lower ($P<0.01$) than the 33 m^{-2} for 1987 (Table 5.7). This increase in the inflorescence density of *Festuca hallii* in 1987 was largely a function of the 1986-to-1987 inflorescence density increases ($P<0.05$) for the control and burnt control treatments (Table 5.8). The inflorescence density for control plants in 1987 was higher ($P<0.05$) than their inflorescence density in 1986 by a factor of 25. The inflorescence density for the plants in the burnt control in 1987 was also higher ($P<0.05$) than their inflorescence density in 1986 by a factor of 3.5. The 1986-to-1987 increase ($P<0.05$) for the inflorescence densities of the control and burnt control treatments with no ($P>0.05$) corresponding annual change for the inflorescence densities of the 1-cut and 2-cut

Table 5.7 Mean square values of the inflorescence density of *Festuca hallii* in the control, burnt control, 1-cut, and 2-cut defoliation treatments for 1986 and 1987.

Source	df	Inflorescence density
Block (B)	9	709
Defoliation (D)	3	4150 **
Error 1 (B x D)	27	637
Years (Y)	1	8283 **
Error 2 (B x Y)	9	381
D X Y	3	4081 **
Error 3 (B x D x Y)	27	599

** indicates significant variances for $P<0.01$.

Table 5.8 Inflorescence density of *Festuca hallii* in the control, burnt control, 1, 2, 4, and 8-cut defoliation treatments, with percentage change the control, burnt control, 2, 4, and 8-cut defoliation treatments over the 1-cut treatment, for 1986 and 1987.

		Density ----(#.m^{-2})----		% change over 1-cut ------(%)------	
Parameter	Defoliation treatment	1986	1987	1986	1987
Inflorescence density	Control	1.9 a*	48.4 ab*	7	227
	Burnt Cntrl	17.0 a*	60.6 a*	60	285
	1-cut	27.1 a	21.3 bc	100	100
	2-cut	5.3 a	2.4 c	19	11
	4-cut	0.2	0.0	1	0
	8-cut	0.0	0.0	0	0

The same letter following means within columns and vegetation groups indicates no significant difference (Bonferroni; $P<0.05$).
An * indicates a significant change between years (Bonferroni; $P<0.05$).
The 4-cut and 8-cut defoliation treatments were not statistically analyzed as they were defoliated prior to the collection of the density data in 1986 and 1987.

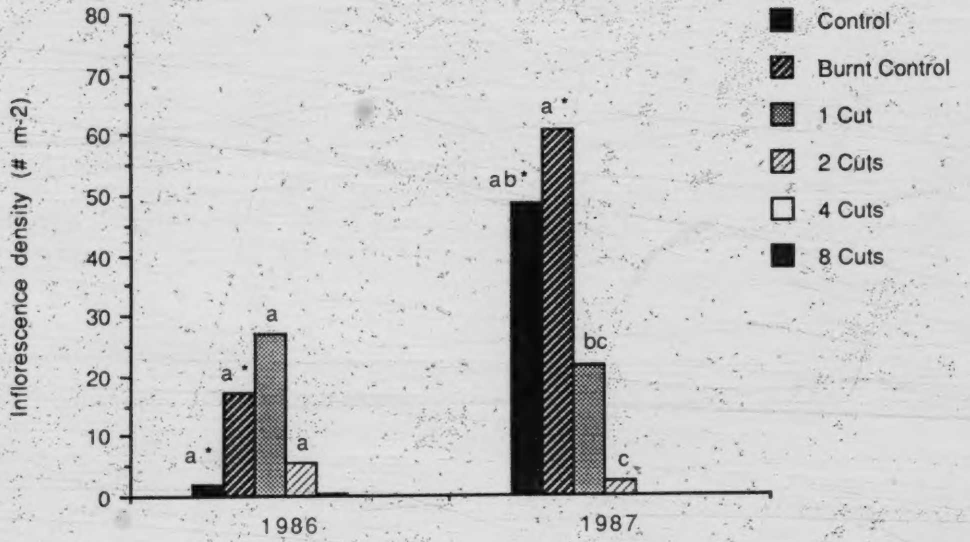

Figure 5.6 Inflorescence density of *Festuca hallii* by defoliation treatment for 1986 and 1987. Different letters above bars indicate significant treatment differences within a year (Bonferroni; $P<0.05$). An * indicates a significant difference between years for that treatment (Bonferroni; $P<0.05$).

defoliation treatments would have contributed to the frequency of defoliation-by-year interaction ($P \leq 0.01$). The year-to-year differences ($P<0.05$) in the inflorescence densities of the control and burnt control treatments likely reflected annual environmental differences which influenced the floral initiation and development of *Festuca hallii.*

There were no ($P>0.05$) differences in inflorescence density for *Festuca hallii* among the defoliation treatments in 1986 (Table 5.8, Figure 5.6). In 1987, the inflorescence density for plants in the burnt control was higher ($P<0.05$) than the inflorescence densities of plants in the 1-cut and 2-cut defoliation treatments. There was a stepwise decrease in inflorescence density with increasing frequency of defoliation for the 1, 2, and 4-cut treatments in both years. Therefore, the frequency of defoliation response ($P<0.01$) was probably a relationship of decreasing inflorescence density with increasing frequency of defoliation (Table 5.7).

Tiller Density

Tiller density was affected ($P \leq 0.001$) by frequency of defoliation (Table 5.9). Because there was no year-to-year effect ($P>0.05$) and no frequency of defoliation-by-year interaction ($P>0.05$), the tiller density results for the two years were combined and reanalyzed with a one-way analysis of variance with significant differences among the means being separated by the Student-Newman-Kuels technique (Table 5.10).

Table 5.9 Mean square values of tiller density, stem base dry matter (DM) weight, stem base total nonstructural carbohydrate (TNC) percentage, stem base TNC pool, and root DM weight to a 7.5 cm depth in the control, burnt control, 1, 2, 4, and 8-cut defoliation treatments for 1986 and 1987.

Source	df	Tiller density	Stem base DM weight	Stem base TNC%	Stem base TNC pool	Root DM weight
Block (B)	9	2801300	38765 **	9.9 ***	641 *	57350
Defoliation (D)	7	7941300 ***	213165 ***	6.1 **	3176 ***	261190 ***
Error 1 (B x D)	63	1411000	15821	1.6	260	46979
Years (Y)	1	954083	20927	36.4 *	1319 **	80642
Error 2 (B x Y)	9	1934400	10822	4.8	59	52263
D X Y	7	671283	34981 *	2.9	780 **	35653 *
Error 3 (B x D x Y)	63	318801	10149	1.3	171	19094

*, **, and *** indicate significant variances for $P<0.05$, 0.01, and 0.001, respectively.

Table 5.10 Tiller density of *Festuca hallii* in the control, burnt control, 1, 2, 4, and 8-cut defoliation treatments, with percentage change of tiller density in the control, burnt control, 2, 4, and 8-cut defoliation treatments over that in the 1-cut defoliation treatment, for the combined 1986 and 1987 data.

Festuca hallii parameter	Defoliation treatment	n	Density (# m^{-2})	% change over 1-cut
Tiller density	Control	10	2509 b	73
	Burnt control	10	3588 a	104
	1-cut	10	3758 a	100
	2-cut	10	3909 a	113
	4-cut	10	3566 a	103
	8-cut	10	2509 b	73

The same letter following means within a column indicates no significant difference (Student-Newman-Keuls; $P<0.05$).

The *Festuca hallii* tiller density for the burnt control was higher ($P<0.05$) than the tiller density for the control in 1986 (Figure 5.7). This increase in tillering was likely a response to changes in the amount and quality of light reaching the base of the plant (Deregibus et al. 1983). In 1987, the *Festuca hallii* tiller density for the 2-cut treatment was higher ($P<0.05$) than that of the 8-cut treatment. The decrease in tiller density for the plants in the 8-cut treatment was likely a response to stress associated with increased frequency of defoliation. The analysis for the combined years indicated that tiller density for plants in the control and the 8-cut treatments were both lower ($P<0.05$) than the tiller densities of plants in the burnt control, 1, 2, and 4-cut treatments (Table 5.10). The results for tiller density for *Festuca hallii* among treatments in 1987 closely represented the tiller density pattern between treatments in the combined analysis (Table 5.10, Figure 5.7).

End-of-season Stem Base Weight, TNC (%), and TNC Pool

The *Festuca hallii* end-of-season stem base DM weight had a season of defoliation-by-year interaction ($P<0.05$) and a season of defoliation response ($P<0.001$), but no year-to-year effect ($P>0.05$) (Table 5.9).

The *Festuca hallii* end-of-season stem base DM weight for the burnt control was higher ($P<0.05$) than the end-of-season stem base DM weights for *Festuca hallii* in all the other treatments, and the

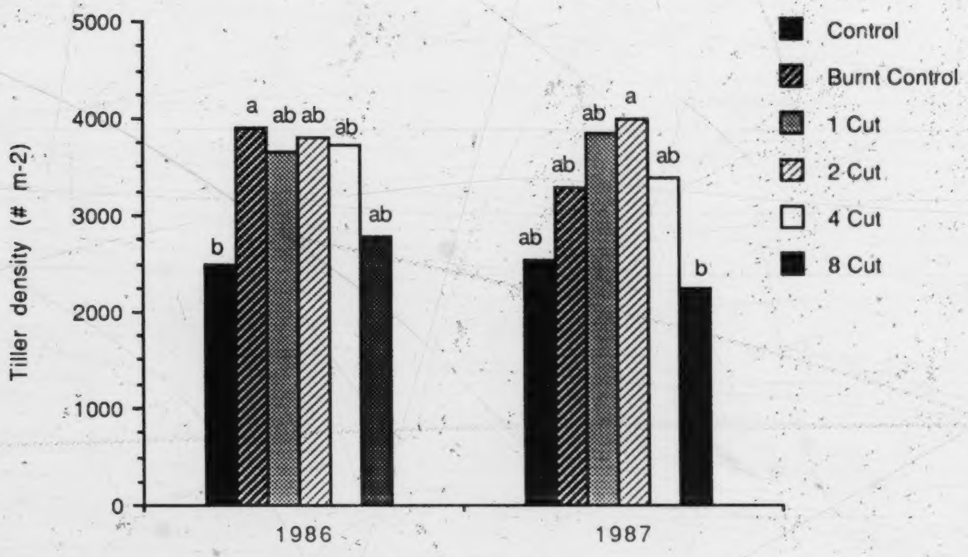

Figure 5.7 Tiller density of *Festuca hallii* by defoliation treatment for 1986 and 1987. Different letters above bars indicate significant treatment differences within a year (Bonferroni; $P<0.05$).

end-of-season stem base DM weight for plants in the 1-cut treatment was higher (P<0.05) than the end-of-season stem base DM weights for plants in the 2, 4, and 8-cut treatments, in 1986 (Table 5.11, Figure 5.8). In contrast, only the end-of-season stem base DM weight for plants in the 1-cut treatment was higher (P<0.05) than the end-of-season stem base weight for plants in the 8-cut treatment in 1987. There was a trend for the end-of-season stem base DM weight to decrease with increasing frequency of defoliation in both years.

There was a 1986-to-1987 decrease (P<0.05) in the end-of-season stem base weight of plants in the burnt control. The values for the end-of-season stem base DM weights for plants in the control, burnt control, and 1-cut treatments were lower in 1987 compared to 1986, while the values for the end-of-season stem base weights for plants in the 2, 4, and 8-cut treatments were higher in 1987 compared to 1986. These year-to-year response differences for the end-of-season stem base DM weights among treatments would have contributed to the frequency of defoliation-by-year interaction (P<0.05) for *Festuca hallii*.

The end-of-season stem base TNC (%) had a year-to-year effect (P<0.05) and a frequency of defoliation response (P<0.01), but no (P>0.05) frequency of defoliation-by-year interaction for *Festuca hallii* (Table 5.9).

Table 5.11 End-of-season (October) stem base dry matter weight, stem base nonstructural carbohydrate (TNC) percentage, and stem base TNC pool of *Festuca hallii* in the control, burnt control, 1, 2, 4, and 8-cut defoliation treatments, with percentage change of stem base dry matter weight, stem base TNC percentage, stem base TNC pool in the control, burnt control, 2, 4, and 8-cut defoliation treatments over that in the 1-cut treatment for 1986 and 1987.

Festuca hallii parameter	Defoliation treatment	1986	1987	% change over 1-cut (%) 1986	% change over 1-cut (%) 1987
		(g m^{-2})			
Stem base DM weight	Control	393 ^{bc}	310 ^{ab}	90	73
	Burnt Cntrl	477 ^{a*}	310 ^{ab*}	109	73
	1-cut	437 ^{b}	427 ^{a}	100	100
	2-cut	249 ^{c}	285 ^{ab}	57	67
	4-cut	173 ^{c}	229 ^{ab}	40	54
	8-cut	179 ^{c}	187 ^{b}	41	44
		(%)			
Stem base TNC (%)	Control	13.9 ^{a}	13.3 ^{a}	105	118
	Burnt Cntrl	13.8 ^{a}	11.7 ^{ab}	105	105
	1-cut	13.2 ^{a}	11.2 ^{b}	100	100
	2-cut	13.3 ^{a}	12.5 ^{ab}	101	112
	4-cut	13.9 ^{a}	13.2 ^{a}	105	118
	8-cut	12.9 ^{a}	12.5 ^{ab}	98	112
		(g m^{-2})			
Stem base TNC pool	Control	55 ^{a}	41 ^{ab}	98	88
	Burnt Cntrl	63 ^{a*}	37 ^{ab*}	111	77
	1-cut	57 ^{a}	47 ^{a}	100	100
	2-cut	32 ^{b}	36 ^{ab}	57	76
	4-cut	23 ^{b}	30 ^{ab}	41	65
	8-cut	23 ^{b}	23 ^{b}	41	49

The same letter following means within a column indicates no significant difference (Bonferroni; $P<0.05$).

An * indicates a significant difference between years for that treatment (Bonferroni; $P<0.05$).

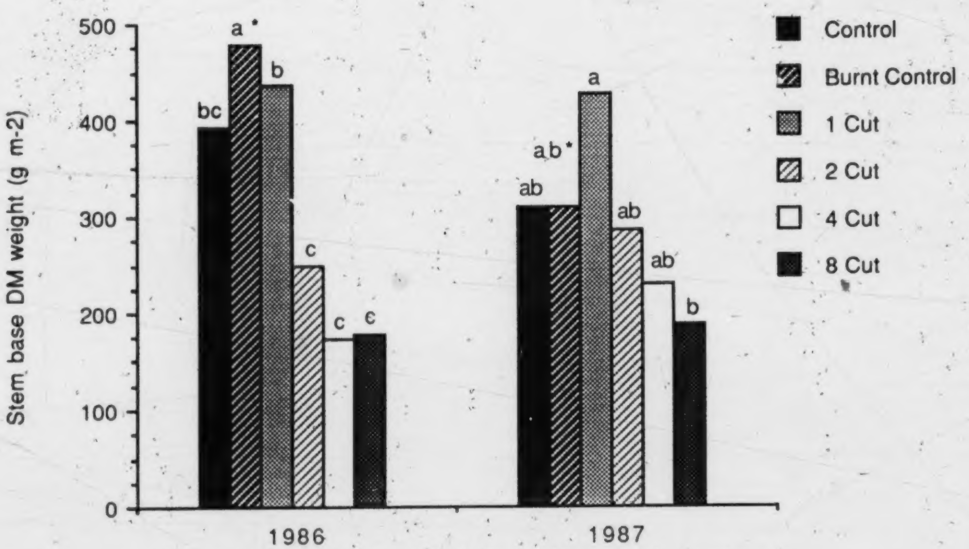

Figure 5.8 End-of-season stem base dry matter (DM) weight of *Festuca hallii* by frequency of defoliation treatment for 1986 and 1987. Different letters above bars within a year indicate significant treatment differences (Bonferroni; P<0.05). An * indicates a significant difference between years for that treatment (Bonferroni; P<0.05).

The end-of-season stem base TNC (%) of 13.5% in 1986 was higher ($P<0.01$) than the 12.4% in 1987. This year-to-year difference in end-of-season TNC (%) may have been associated with the degree of winter hardening as influenced by the average September temperature, which in 1986 was 8.5° C (1.9° C below normal), while in 1987 it was 13.3° C (2.9° C above normal) (Table 2.4).

Analysis of variance indicated a frequency of defoliation effect ($P<0.01$) for the end-of-season stem base TNC (%) (Table 5.9). Multiple means separation, however, indicated no differences ($P>0.05$) among defoliation treatments for the end-of-season stem base TNC (%) of *Festuca hallii* in 1986 (Table 5.11, Figure 5.9). In 1987, however, the end-of-season stem base TNC (%) for the *Festuca hallii* plants in the control and 4-cut treatment defoliation treatments were higher ($P<0.05$) than the TNC (%) values for the plants in the 1-cut defoliation treatment. In both years there was a stepwise increase in end-of-season stem base TNC (%) with increasing frequency of defoliation for plants in the 1, 2, and 4-cut defoliation treatments, but this stepwise increase was then followed by a decrease in the end-of-season stem base TNC (%) for plants in the 8-cut treatment. While the magnitude of the end-of-season stem base TNC (%) differences for *Festuca hallii* among treatments in 1986 was not as great as in 1987, the pattern of differences was similar. The comparatively high end-of-season TNC (%) values for plants from the control and 4-cut defoliation

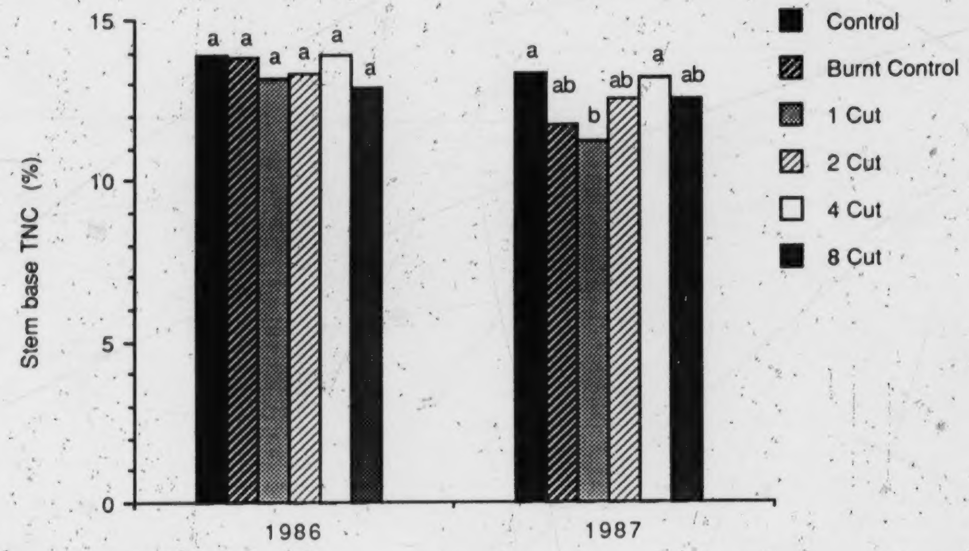

Figure 5.9 End-of-season stem base total nonstructural carbohydrate percentage (TNC (%)) of *Festuca hallii* by defoliation treatment for 1986 and 1987. Different letters above bars within a year indicate significant treatment differences (Bonferroni; $P<0.05$).

treatments, and the comparatively low end-of-season TNC (%) values for plants from the 1-cut defoliation treatment, was consistent for both years and would have contributed to the frequency of defoliation response ($P<0.01$).

The end-of-season stem base TNC pool of *Festuca hallii* had a frequency of defoliation-by-year interaction ($P<0.01$), a year-to-year effect ($P<0.01$), and a frequency of defoliation response ($P<0.01$) (Table 5.9).

The *Festuca hallii* end-of-season stem base TNC pool treatment average in 1986 of 42.3 g m^{-2} was higher ($P<0.01$) than the 35.7 g m^{-2} for 1987 (Table 5.9). This decrease in the end-of-season stem base TNC pool in 1987 was likely a function of both the 1986-to-1987 decrease ($P<0.05$) in the end-of-season stem base weight for plants in the burnt control, and the overall 1986-to-1987 decrease ($P<0.01$) in the end-of-season TNC (%) treatment average (Table 5.11). The combination of these two factors certainly contributed to the 1986-to-1987 decrease ($P<0.05$) in the end-of-season TNC pool for the plants in the burnt control, and to the overall year-to-year decrease ($P<0.01$) for the end-of-season stem base TNC pool treatment average (Figures 5.8, 5.9, 5.10).

The end-of-season stem base TNC pool for the plants in the control, burnt control, and 1-cut defoliation treatments were higher ($P<0.05$) than the end-of-season stem base TNC pool for the plants in the 2, 4, and 8-cut defoliation treatments in 1986 (Table

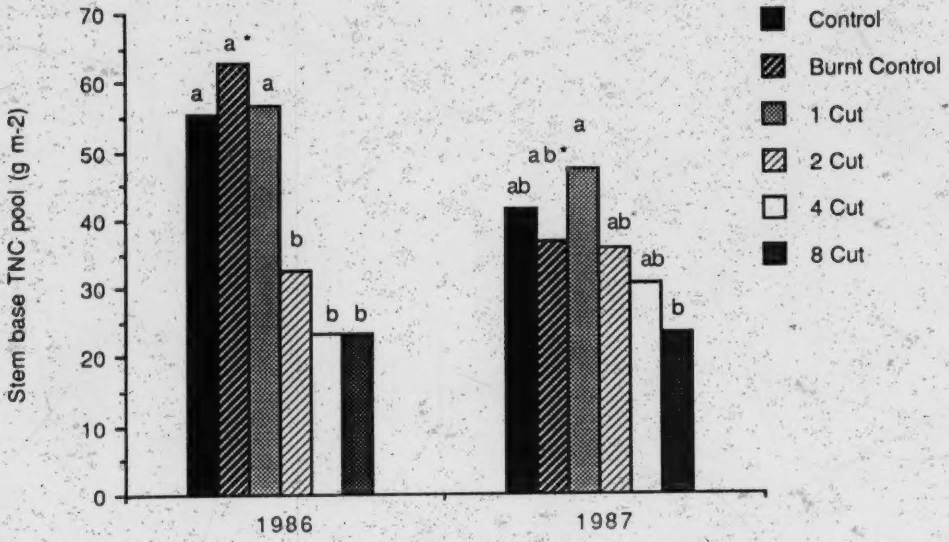

Figure 5.10 End-of-season stem base total nonstructural carbohydrate (TNC) pool of *Festuca hallii* by defoliation treatment in 1986 and 1987. Different letters above bars within a year indicate significant treatment differences (Bonferroni; $P<0.05$). An * indicates a significant difference between years for that treatment (Bonferroni; $P<0.05$).

5.11, Figure 5.10). In 1987, the end-of-season stem base TNC pool for the plants in the burnt control was higher ($P<0.05$) than the end-of-season stem base TNC pool for the plants in the 8-cut defoliation treatment only. In both years, there was a stepwise decrease in the end-of-season stem base TNC pool with increasing frequency of defoliation for the 1, 2, and 8-cut defoliation treatments which would have contributed to the frequency of defoliation effect ($P<0.001$) (Table 5.9). However, the year-to-year changes in the end-of-season stem base TNC pools among the different treatments would have also contributed to the frequency of defoliation-by-year interaction ($P<0.01$).

Root Weight

The *Festuca hallii* end-of-season root DM weights to a 7.5 cm depth had a season of defoliation-by-year interaction ($P<0.05$) and a season of defoliation response ($P<0.001$), but no year-to-year effect ($P>0.05$) (Table 5.9).

The values for the root DM weights for plants in the control and burnt control were lower in 1987 than in 1986, while the values for the root DM weights for plants in the 1, 2, 4, and 8-cut defoliation treatments were all higher in 1987 compared to 1986. These year-to-year differences in the response of the root DM weights of the *Festuca hallii* plants among treatments would have contributed to the frequency of defoliation-by-year interaction ($P<0.05$).

The *Festuca hallii* end-of-season root DM weights to a 7.5 cm depth for plants in the burnt control and 1-cut defoliation treatments were higher ($P<0.05$) than the root DM weights for plants in the 4-cut defoliation treatment in 1986 (Figure 5.11). There were no ($P>0.05$) differences for the end-of-season root DM weights of the plants among the treatments in 1987, but the pattern of response for the root DM weights of the plants from the different treatments remained similar to that of 1986. This similarity would have contributed to the strong frequency of defoliation response ($P<0.001$).

There was a stepwise decrease in end-of-season root DM weights to a 7.5 cm depth with increasing frequency of defoliation for the plants in the 1, 2, and 4-cut defoliation treatments in both years (Figure 5.11). The response pattern for the end-of-season root DM weights to increasing frequency of defoliation was reciprocal to the pattern of response for the end-of-season stem base TNC (%) in relation to increasing frequency of defoliation (Figure 5.9).

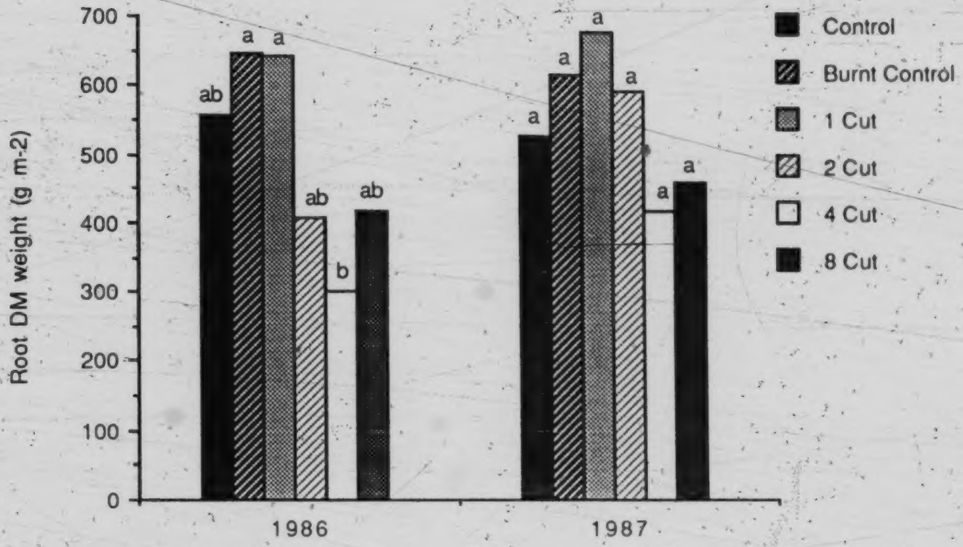

Figure 5.11 End-of-season root dry matter (DM) weight to a 7.5 cm depth of *Festuca hallii* by defoliation treatment for 1986 and 1987. Different letters above bars within a year indicate significant treatment differences (Bonferroni; $P<0.05$).

DISCUSSION

Sward Responses - Yield and Sward Composition

The effect of frequency of defoliation on aboveground DMY was reflected only in the total sward (P<0.001) and *Festuca hallii* (P<0.001) responses (Table 5.2). In this three year study, the aboveground DM yields of the other grasses and grass-like species, forbs, and woody components did not respond (P>0.05) to frequency of defoliation. In a mature grass sward composed mostly of perennials, one would expect a relatively slow change in sward composition in response to frequency of defoliation differences, and that is what occurred.

The total sward aboveground DMY and the aboveground DM yields of each sward component were significantly different between the years (Table 5.2). This year-to-year difference appears to be associated with the reduced precipitation in 1987 compared to 1986 as detailed in the results section (Tables 2.2, 2.3). These precipitation differences were particularly critical in 1987 for the months of June and July. Both 1986 and 1987 had less precipitation than the long term average, but precipitation during the critical growth period of June and July in 1987 was only 56% and 73% of that received during the same month in 1986. For a frequency of defoliation experiment limited to a mid-May to late August time frame, the amounts of annual June and July precipitation would likely be critical to accumulated DM yields.

Therefore, annual precipitation differences were likely a major contributing factor to the significant year effect giving the reduced total sward DMY and the reduced DMY for each of the sward components in 1987 compared to 1986 (Table 5.3).

Bittman and Simpson (1987) used rain-out shelters to demonstrate with *Bromus inermis*, *Leymus angustus*, and *Agropyron cristatum* a plateauing of DMY by the beginning of July for water stressed versus watered treatments. With a July 15th defoliation they also demonstrated a pronounced decrease of mid-summer regrowth for water stressed versus watered treatments. These results also suggest that July precipitation is critical not only for the continued growth but the regrowth of defoliated grasses during the midsummer in the parkland region of Western Canada.

In this study, if 1987 were considered a water stressed year in contrast to 1986 as a watered year, the year-to-year differences in the accumulated regrowth for the 4-cut and 8-cut frequency of defoliation treatments clearly suggest the strategic importance of adequate precipitation from late May to early July for *Festuca hallii* regrowth. If the period of maximum crop growth rate for *Festuca hallii* is from early May through June (Chapter III), then it would be reasonable to suggest that the presence or absence of precipitation at this time would greatly influence the subsequent total annual dry matter production. This hypothesis would appear to be supported in this study by the year-to-year differences in total DMY and the accumulated DMY. Therefore, timing of growing season precipitation, especially during June, would be of critical importance for both regrowth and the total annual dry matter production for defoliation frequencies of 4 or more cuts per season.

There was a frequency of defoliation-by-year interaction for the DM yields of the total sward (<0.001), *Festuca hallii* (P<0.05) and forb (P<0.05) components (Table 5.2). For the frequency of defoliation treatments, the decrease in 1987 DMY was least dramatic for the 4-cut, moderate for the 2-cut, and greatest for the 1-cut or 8-cut for the total sward and *Festuca hallii* which may explain the frequency of defoliation-by-year interactions (Tables 5.3, Figures 5.1, 5.2). These year-to-year differences may also lend support to the theory that moderate defoliation during times of drought stress may actually enhance DMY by reducing transpiration (Mohammad et al. 1982). There was a suggestion of this for *Festuca hallii* with the slight increase in DMY for the 2-cut treatment compared to that for the 1-cut treatment in 1987.

The results of this study showed that the aboveground DMY of *Festuca hallii* was negatively affected (P<0.001) by increasing frequency of defoliation (Tables 5.2, 5.3, Figure 5.2). This indicated that *Festuca hallii* occupies the role of a classic decreaser in the *Festuca-Stipa* grassland (Wroe et al. 1988). Therefore, *Festuca hallii* was the key species at this location. What the optimum number of cuts per season is will require further study, but this work suggested that it was the 2-cut treatment.

This is consistent with work by Willms (1983) in southwestern Alberta who found that the optimum rest interval between cuttings for maximum DMY for *Festuca campestris* at a cutting height of 5.0 cm was greater than 8 weeks. He found that a 4-week rest interval was only optimal when the defoliation height was greater than 15 cm. Therefore, it could be reasonably concluded that in terms of repeated intense defoliations at a height of 3 cm, the rest interval must be equal to or greater than 8 weeks for optimum DMY of *Festuca hallii*.

Festuca hallii sward composition decreased (P<0.001) with increasing frequency of defoliation (Tables 5.5, 5.6, Figure 5.5). For the other grasses and grass-like species component and the forb component there was a general increase in sward composition with increasing frequency of defoliation. The decrease in the *Festuca hallii* sward composition is a reflection of its decreasing aboveground DMY in response to increasing frequency of defoliation (Tables 5.2, 5.3, Figure 5.2).

In contrast, increasing frequency of defoliation resulted in increases in the sward composition of the other grasses and grass-like species (P<0.05) and forb (P<0.05) components (Tables 5.5, 5.6). These increases in sward composition were not associated with any increase (P>0.05) in the DMY of the other grasses and grass-like species or forbs, but with a decrease (P<0.001) in DMY for *Festuca hallii* with increasing frequency of defoliation (Tables 5.2, 5.3, Figure 5.2). An increase in DMY for the other grasses and grass-like species and for the forbs with increasing defoliation frequency may have developed if these treatments had been repeated annually for an experimental period greater than three years, thereby enhancing their competitive position further relative to that of *Festuca hallii*.

These results emphasized the relative sensitivity of *Festuca hallii* to frequency of defoliation when compared with the other grasses and grass-like species component and the forb component (Tables 5.2, 5.3, 5.5, 5.6). The aboveground DMY and sward composition responses of the other grasses and grass-like species and forb components appeared to be comparatively resistant to adverse effects of increasing frequency of defoliation. The differences in these responses for these sward components to increasing defoliation underscore *Festuca hallii* as the key indicator species upon which management of a *Festuca-Stipa* grassland in central Alberta should be based (Wroe et al. 1988).

Festuca hallii **Responses - Morphological and Physiological**

The year-to-year effect ($P<0.01$) and the frequency of defoliation-by-year interaction ($P<0.01$) for the inflorescence densities of *Festuca hallii* are likely explained by the 1986-to-1987 differences ($P<0.05$) in the inflorescence densities of the plants in the control and burnt control treatments (Tables 5.7, 5.8, Figure 5.6). The 1987 inflorescence density of the plants in the control increased 25 times over that of 1986, and the 1987 inflorescence density of the plants in the burnt control increased 3.5 times over that of 1986. This indicates a pronounced year-to-year variability for the inflorescence density of nondefoliated *Festuca hallii* plants.

Johnston and MacDonald (1967) showed that floral initiation for *Festuca campestris* in southwestern Alberta was erratic. They showed that partial initiation occurred in the period between August and September in the year prior to bolting. Floral initiation for *Festuca hallii* can also be erratic as shown by work by Bailey and Anderson (1978) and the year-to-year differences in inflorescence densities of *Festuca hallii* as demonstrated in this study (Tables 5.7, 5.8, Figure 5.6). Given the close relationship between *Festuca hallii* and *Festuca campestris* (Pavlick and Looman, 1984), it is reasonable to assume that floral initiation for *Festuca hallii* also occurs in the late summer prior to the year of bolting.

Pearson and Ison (1987) have summarized how complicated, poorly understood, and species specific the mechanisms governing floral initiation are. One possible hypothesis for explaining floral initiation in *Festuca hallii* is suggested below. This hypothesis, however, does not account for possible prerequisite interactions with daylength, temperature, light intensity, or light quality.

If floral initiation begins in August or September of the previous year (Johnston and McDonald 1967); the results of this study suggest that there was some 1985-to-1986 differences which did not favor floral initiation for the control in 1986 but did in 1987 (Tables 5.7, 5.8, Figure 5.6). Monthly precipitation amounts were 25%, 121%, and 87% of the long term average for July, August, and September in 1985 (Table 2.2). In 1986, precipitation was 134%, 36% and 168% of the long term average for July, August, and September. During the 1985 July to September period the soil moisture would have been continuously low. During this same period in 1986, the plants experienced a high soil moisture condition in July, a low soil moisture condition in August, and a high soil moisture situation in September. The low moisture situation during August may have acted as a stress trigger for floral initiation, while the high moisture situation in September may have then facilitated the development of any floral primordia initiated in August.

The pattern of inflorescence densities between the 1, 2, 4, and 8-cut treatments was the same for both years (Table 5.8, Figure 5.6). This study also showed that defoliation frequencies of 2 or more cuts per season resulted in the essential elimination of inflorescence production for *Festuca hallii.* Therefore, if an increase in inflorescence density is a grazing management objective, defoliation should be limited to 1-cut per season and that defoliation should be deferred as close to the beginning of October as is reasonable (Chapter IV).

Tillering in grasses may be regulated by release from apical dominance, temperature, light quantity, light quality, resource availability within and between tillers, and leaf or root produced growth regulators (Richards et al. 1988). Decreasing tiller density with increasing frequency of defoliation has been demonstrated on *Panicum hemitomon* in Florida (Kalmbacher and Martin 1988). Willms (1988) has also shown that an increase in the tillering density of *Festuca campestris* was likely caused by an increase in photosynthetically active radiation near the crown following defoliation.

In this study plants from the burnt control, 1, 2 and 4-cut treatments all had higher (P<0.05) tiller densities than the plants in the control and 8-cut treatments (Table 5.10). A high amount of litter, a lower degree of light penetration and lower red light levels at the stem bases, lower soil and stem base temperatures, and higher soil water would be characteristic of the control compared with plants in the burnt control and other treatments. The results of this frequency of defoliation study suggested that for *Festuca hallii* there was a trend for tiller density to increase with only 1 or 2-cuts per season and a minimum rest duration of eight weeks when compared to plants in the control and burnt control. This probably reflected increasing light penetration and greater far red light levels at the stem base (Deregibus et al. 1983, Willms 1988), and enhanced stem base and soil temperatures associated with the regular removal of forage and litter by mowing. These results suggested that a 2-cut defoliation system with a minimum rest duration of eight weeks may provide maximum tiller density for *Festuca hallii*.

Tiller density appeared to be sensitive to litter buildup as demonstrated in the 1986-to-1987 differences for plants in the control and burnt control (Figure 5.7). It is important to note that the plants in the burnt control demonstrated a significant increase in tillering in 1986 over the plants in the control, but not in 1987. This may have reflected a loss of tillering stimulus caused by the annual buildup of litter and associated decrease in light penetration to the stem base of the plants in the burnt control subsequent to its initial defoliation by fire in May of 1985.

Tiller density of *Festuca hallii* was surprisingly robust to the stress associated with increasing frequency of defoliation. The plants in the 8-cut treatment had an identical tiller density to those in the control and this was a decrease ($P<0.05$) in tiller density compared to the plants in the burnt control and other defoliation treatments (Table 5.10). This decrease ($P<0.05$) in tiller density for *Festuca hallii* in the 8-cut treatment would be a function of stress associated with increasing frequency of defoliation, and therefore caused by different factors than those limiting tiller density of plants in the undisturbed control. Therefore, it would appear that tiller density was more resistant to the stress associated with increasing frequency of defoliation than the DMY or sward composition of *Festuca hallii*.

It is noteworthy that tiller density of *Festuca hallii* was not affected by the year-to-year precipitation differences suggesting that it is a parameter which operated independently of the level of moisture stress experienced in 1987. Tiller density may therefore provide a robust indicator for determining when severe defoliation stress is being placed on *Festuca hallii*, independent of annual precipitation differences.

In 1986, the end-of-season stem base weight for *Festuca hallii* plants in the burnt control was higher ($P<0.05$) than that in all the other treatments (Figure 5.8). This could be a result of the increased tiller production in the 1986 burnt control (Figure 5.7) which was likely caused by the defoliation effect of the May 1985 burn (Sinton and Bailey 1980, Willms et al. 1986) which would have subsequently optimized photosynthate production and storage in the absence of any defoliation stress.

There was a 1986-to-1987 reduction ($P<0.05$) for the end-of-season stem base weight of the plants in the burnt control (Table 5.11, Figure 5.8). This 1986-to-1987 reduction ($P<0.05$) in end-of-season stem base weight coincided with a 1986-to-1987 increase ($P<0.05$) in inflorescence density for the plants in the burnt control (Table 5.8, Figure 5.6). A similar 1986-to-1987 increase ($P<0.05$) in inflorescence density was demonstrated by the plants in the control which was also associated with a 1986-to-1987 decrease in their end-of-season stem base weight. For plants in the 1-cut defoliation treatment there was neither a year-to-year change in their inflorescence density nor their end-of-season stem base weight. This suggests that the 1986-to-1987 reductions in the end-of-season stem base weights for the plants in the control and burnt control was associated with the 1986-to-1987 increases in their inflorescence densities.

The 1-cut defoliation treatment placed the least energy drain on stem base reserves of *Festuca hallii* in 1987 because the inflorescence density for *Festuca hallii* plants in the 1-cut treatment was suppressed when compared to the enhanced inflorescence density of plants in the control and burnt control in 1987, and the 1-cut treatment would have imposed the least defoliation stress of the different frequency of defoliation treatments. Therefore, it would be logical for the plants in the 1-cut frequency of defoliation treatment to have the highest 1987 end-of-season stem base weight (Figure 5.8). This highest end-of-season stem base weight was higher ($P<0.05$) than that for the plants in the 8-cut frequency of defoliation treatment only in 1987. Both years are consistent in terms of increasing frequency of defoliation resulting in significantly lower end-of-season stem base weights, with the greatest reduction occurring between plants in the 1 to 2-cut defoliation treatments. Similar reduction patterns with increasing frequency of defoliation have been shown for crown weights of *Elymus junceus* (Thaine 1954) and rhizome weights of *Panicum hemitomon* (Kalmbacher and Martin 1988).

Total nonstructural carbohydrates (TNC) in forage grasses include reducing sugars, nonreducing sugars, fructan, and starch. These substances appear to be the primary energy reserves utilized by grasses for growth and dormant season maintenance. The role and importance of stem base TNC reserves in the initiation of spring growth or regrowth following defoliation is currently being debated and would appear to vary from species to species (Richards and Caldwell 1985). Historically, emphasis has been placed on stem base TNC reserves for species vigor and regrowth (White 1973). More recent work has shown that the TNC storage in other organs, the photosynthetic capacity and the physiological mechanism of resource allocation for individual species are also important factors in determining the ability of species to overwinter and tolerate defoliation (Caldwell et al. 1981) However, stem base TNC concentration remains an important technique for evaluating forage grass energy reserves, especially when the concentration is used to determine the stem base TNC pool by multiplying by the stem base DM weight (Volenec 1986, Richards and Caldwell 1985).

The end-of-season stem base TNC (%) of *Festuca hallii* was affected (P<0.01) by the frequency of defoliation treatments (Table 5.6). In 1986 there was no significant multiple means separation between the controls and defoliation treatments, but there was in 1987 with the control and 4-cut defoliations being significantly higher than the 1-cut (Table 5.11, Figure 5.9). This difference could be associated with differences in late summer and autumn root growth between the frequency of defoliation treatments. This is suggested by the end-of-season root DM weights having a pattern which is the mirror image of the end-of-season TNC (%) results for the frequency of defoliation treatments (Figures 5.9, 5.11).

The year effect ($P<0.05$) for the end-of-season stem base TNC (%) was likely associated with September 1986 being 1.9° C below the long term monthly temperature average, whereas September 1987 was 2.9° C above the long term monthly temperature average (Tables 2.3, 5.9). The lower September 1986 temperature would likely lead to a higher degree of winter hardening and therefore higher TNC (%) values for October 1986 compared to October 1987. George et al. (1989) showed a 5% year-to-year difference for October stem base TNC (%) for *Panicum virgatum* across six treatments similarly applied across both years which they attributed to year-to-year weather differences.

The end-of-season TNC (%) for the plants in the burnt control was 15 % lower in 1986 compared to 1987 while the end-of-season TNC (%) for the plants in all the other 1987 treatments were 4% to 6% lower than in 1986 (Table 5.11, Figure 5.9). This greater reduction in the end-of-season stem base TNC (%) for plants in the burnt control compared to the end-of-season stem base TNC (%) for plants in the other treatments may be associated with the high inflorescence density for plants in the burnt control compared to the inflorescence density for plants in the other treatments in 1987 (Figures 5.6). In both years the plants in the control and the 4-cut defoliation treatments had the highest end-of-season TNC (%) values. In general, the decreasing end-of-season TNC (%) treatment differences expected with increasing frequency of defoliation were not observed.

The 1986-to-1987 reductions in the end-of-season TNC pool for plants in the control and burnt control likely reflected, in part, their high inflorescence production in 1987 as noted above (Figures 5.7, 5.10). This study clearly showed that increasing frequency of defoliation reduced the end-of-season stem base TNC pool, versus end-of-season TNC (%), by the reduction of the end-of-season stem base weight of the plants. In both years the end-of-season TNC pool for plants in the 8-cut treatment was more than 50% lower than that for the plants in the 1-cut treatment (Table 5.11). Thaine (1954) showed a similar reduction of the TNC pool with increasing frequency of defoliation for *Elymus junceus*.

The results of this study for the end-of-season stem base TNC pool are complicated by significant year and frequency of defoliation treatment by year interactions, but they do indicate that even 2 cuts per season will reduce the stem base TNC pool between 25% and 40% compared to a single cut per season. These results suggest that in terms of end-of-season stem base weight and TNC pool, *Festuca hallii* is most suited to a single intense annual defoliation. The 4 and 8-cut defoliation treatments were clearly the most damaging to the end-of-season stem base weight and TNC pool. Therefore, these end-of-season stem base weight and TNC pool results suggest that *Festuca hallii* may be well adapted to either a single or 2 widely spaced intense annual defoliations.

Tainton (1958) demonstrated with *Themeda triandra* in South Africa that increasing frequency of defoliation can reduce root growth. The data for the combined years for this frequency of defoliation study indicated that the 4 and 8-cut defoliation treatments significantly reduced the *Festuca hallii* end-of-season root dry matter weight to the 7.5 cm depth when compared to the burnt control and 1-cut defoliation treatments. The reduction for the 4 and 8-cut defoliation treatments would appear to be a clear response to defoliation stress. Crider (1955) illustrated how *Chloris gayana* root growth may be progressively delayed or stopped by defoliation intensity. However, Richards (1984) showed in a study of *Agropyrpn desertorum* and *Agropyron spicatum* that the root growth response of a particular grass to defoliation stress is species specific.

In this study with *Festuca hallii*, a low frequency of defoliation such as the one time burn, or the single annual defoliation, appeared to enhance root growth over that of the 4-cut and 8-cut defoliation treatments (Figure 5.11). This root growth response to the frequency of defoliation treatments again suggests that *Festuca hallii* is a species optimally suited to only one or two widely spaced defoliations per growing season versus multiple defoliations or heavy continuous grazing.

Defoliation Treatment Effects

This study provided the opportunity to look at what effects a single burn had on the sward dynamics, and the responses of

Festuca hallii when compared to the undisturbed control and the frequency of defoliation treatments. The burnt control treatment was an otherwise undisturbed plot in the experimental blocks which were created by the prescribed burn conducted on May 3, 1985. The prescribed burn was used to clear the litter buildup from the approximate 25 years of previously undisturbed growth within the experimental blocks used for this study. Sinton and Bailey (1980) demonstrated that a burn has very similar effects to mowing on *Festuca hallii*.

By 1987 the *Festuca hallii* sward composition for the burnt control was higher (P<0.05) than that of the control and the frequency of defoliation treatments (Figure 5.5). This increase likely reflected a stimulation of growth of *Festuca hallii* in the burnt control which was not expressed untill the second year after the burn. There was an increase in tiller density (P<0.05), and also an increase in end-of-season stem base DM weight (P<0.05), for the plants in the burnt control over those in the control in 1986, which was only one year after the burn (Figures 5.7, 5.8). In 1986 and 1987 there was a suggestion that the burn increased inflorescence density of the plants in the burnt control compared to those in the control (Figure 5.6). These effects taken together suggest that an appropriate prescribed burn could be used to enhance the sward composition, tiller density, end-of-season stem base DM weight, and inflorescence density of *Festuca hallii* in an underutilized *Festuca-Stipa* grassland. This suggests that prescribed burning could be used as a rejuvenation tool for underutilized *Festuca-Stipa* grasslands.

This study demonstrates that overall, the 1-cut defoliation treatment has the minimum detrimental effect on *Festuca hallii* compared to the 2, 4, and 8-cut defoliation treatments (Figures 5.2, 5.5, 5.6, 5.8, 5.10, 5.11). The change from the 1-cut to 2-cut defoliation treatments resulted in a 38% reduction in the end-of-season stem base DM weight and a 34% reduction in TNC pool when the results were averaged for both years (Table 5.11). These results suggest that in terms of management for a vigor rest, *Festuca hallii*, may require intermittently a year in which defoliation is limited to a single event. The results of the season of defoliation study indicate that a single annual defoliation after early September would have the minimum impact, and therefore the greatest benefit, in terms of a vigor rest for *Festuca hallii* (Chapter IV). Within the seasonal time frame in which this frequency of defoliation study was carried out, the 4-cut and 8-cut defoliation treatments resulted in a significant loss of production yield, a loss of range condition, a negative range trend, and a vigor reduction for *Festuca hallii*. This indicates that within the framework of this study, the 1-cut and 2-cut defoliation frequencies are optimal for maximizing aboveground DMY while simultaneously maintaining the vigor of *Festuca hallii* and the range condition of this *Festuca-Stipa* grassland.

In summary, this study strongly suggests that *Festuca hallii* is the type of native grass species that, in central Alberta, may be well suited to a high intensity low frequency type of grazing management system, provided that it has a minimum vigor rest of eight weeks. Further work is required to determine the optimum period of rest for this species for defoliation intervals which are staggered at other periods of the growing season.

CONCLUSIONS

There was a trend for total annual DMY, end-of-season stem base DM weight, end-of-season TNC pool, and end-of-season root DM weight to a 7.5 cm depth of *Festuca hallii* to be reduced when the frequency of defoliation exceeded 2-cuts per season with a minimum rest duration of eight weeks after three consecutive years of treatment application. In contrast, increasing frequency of defoliation had no effect on the annual DMY for the other sward components of the other grasses and grass-like species, forbs and woody species.

Sward composition (DM %) for *Festuca hallii* was reduced while sward composition of the other grasses and grass-like species and forb species were increased with increasing frequency of defoliation which indicated that *Festuca hallii* acted as a classic decreaser in this *Festuca-Stipa* grassland.

Inflorescence production of *Festuca hallii* was virtually eliminated with more than one late summer defoliation while tiller density of *Festuca hallii* was optimized with 2-cuts per season and a minimum rest duration of eight weeks.

While increasing frequency of defoliation reduced the end-of-season stem base weight and the end-of-season TNC pool of *Festuca hallii*, this relationship was not expressed for the end-of-season TNC (%). Therefore, end-of-season stem base DM weight could be used as a simple index of defoliation stress for *Festuca hallii*.

Prescribed burning may be a management option for rejuvenating litter bound or undergrazed *Festuca-Stipa* grasslands.

Festuca hallii may be well adapted to a high intensity, low frequency type of defoliation system.

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VI. VIGOR OF PLAINS ROUGH FESCUE UNDER VARIOUS SEASONS AND INTENSITIES OF GRAZING IN CENTRAL ALBERTA

INTRODUCTION

Plant vigor is an estimate of the health of a plant in comparison to other individuals of the same species (Society for Range Management 1989). Vigor is estimated by the measurement of one or more plant attributes. Changes in plant vigor in response to different grazing regimes can provide a measure of defoliation stress. This type of information can be of value in the overall development of management plans for the key species of a grassland.

Etiolated regrowth is one technique which has been used to evaluate the effect of grazing, or defoliation, on the vigor of a forage species (Edwards 1965). This method is based on the assumption that the vigor of a plant can be estimated by the amount of etiolated regrowth after the plant's leaves have been removed. Etiolated regrowth as a measure of a plant's vigor or carbohydrate reserves has been used by a number of workers with several forage species.

Edwards (1965), and Bailey and Mappledoram (1983), used etiolated regrowth as a technique for evaluating the vigor of warm-season grasses following various grazing treatments in

South Africa. Dovrat et al. (1972) used etiolated regrowth to investigate the influence of defoliation and nitrogen on *Chloris gayana*. Young and Evans (1978) used etiolated regrowth to evaluate the response of *Agropyron desertorum* to mowing and atrazine treatments. A reduction in etiolated regrowth with increasing frequency of clipping was demonstrated for *Festuca rubra*, *Heracleum sphondylium*, and *Taraxacum officinale* by Willoughby (1986) . Etiolated regrowth has also been used to evaluate plant vigor of *Medicago sativa* (Langille et al. 1965, Stout 1984, McKenzie et al. 1988). In all cases the amount of etiolated regrowth was used as an estimate of either the plant's nonstructural carbohydrate reserves or vigor. There is evidence, however, that while the amount of etiolated regrowth after defoliation may be a measure of a plant's vigor, it is not necessarily correlated with the amount of nonstructural carbohydrate reserves in the stem bases and roots of the plant (Richards and Caldwell 1985, McKenzie et al. 1988).

Festuca hallii (Vasey) Piper[1] is the key species in the *Festuca-Stipa* grasslands of central Alberta (Pavlick and Looman 1984, Wroe et al. 1988). This native grassland has been shown to have forage production equal to, or better than, the forage production of introduced *Bromus inermis-Festuca rubra* grasslands in the absence of a legume (Bailey et al. 1980a). Average daily gains for steers of 1.1 kg under light (8 AUM) June grazing and 0.8 kg under light (8 AUM) autumn grazing on *Festuca-Stipa* grassland has been shown over a 11-year grazing study by Bailey et al. (1988). Most of this weight gain performance was attributable to *Festuca hallii* which may contribute more than 70% of the forage dry matter yield from *Festuca-Stipa* grasslands of central Alberta.

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[1] Scientific nomenclature follows Moss (1983) except where a different authority is cited in the text.

There has been some confusion in both the taxonomy and nomenclature of the North American rough fescues (Pavlick and Looman 1984, Harms 1985). Historically, the key species in the *Festuca-Stipa* grasslands of the aspen parkland of central Alberta and the *Festuca-Danthonia* grasslands of the Rocky Mountain foothills of south-western Alberta, has been called *Festuca scabrella* (Moss 1983). The rough fescues of these two regions have been commonly distinguished as the plains rough fescue and foothills rough fescue, respectively. The species nomenclature for the North American rough fescues as proposed by Pavlick and Looman (1984) will be followed in this paper with the plains rough fescue identified as *Festuca hallii* (Vasey) Piper and the foothills rough fescue as *Festuca campestris* Rydb.. When literature cited refers to *Festuca scabrella,* an effort will be made to interpret that literature as *Festuca campestris* or *Festuca hallii* on the basis of the geographic distribution of taxa as presented by Pavlick and Looman (1984) and Harms (1985).

The sensitivity of fescue grasslands to defoliation has been noted since the early ecological survey work in Alberta (Moss and Campbell 1947). A season of defoliation effect with a greater vulnerability to spring defoliation than to autumn defoliation has been demonstrated for *Festuca campestris* in south-central British Columbia (McLean and Wikeem 1985) and *Festuca hallii* in central Alberta (Bailey and Anderson 1978). Where *Festuca-Stipa* grasslands have been grazed with a high compared to low stocking rate, the canopy cover (%) and forage production of *Festuca hallii* has decreased (Bailey et al. 1988). Therefore, there are indications of changes in the vigor of *Festuca hallii* in response to differences in both season of defoliation and intensity of defoliation.

The purpose of this study was to determine how the season and intensity components of five long term grazing regimes (Light June, Heavy June, Heavy Continuous, Heavy Autumn and Light Autumn) affected the vigor of grazed versus nongrazed *Festuca hallii* in central Alberta using etiolated regrowth as a measurement technique.

MATERIALS AND METHODS

Study Area and Experimental Design

The study area (53°N latitude and 112°W longitude) was located on Section 28 of the University of Alberta's research ranch approximately 150 km southeast of Edmonton, Alberta. The climate is a cold-temperate Boreal climate (Walter 1979) with an average annual temperature of 1.9°C and a total average annual precipitation of 432 mm, of which 323 mm or 75% falls mostly as rain between April and September. Elevation is approximately 700 m above sea level. The grassland soils are predominantly thin Orthic Black Chernozems (Howitt 1988). The grazing season is traditionally from April to December depending upon the plant species being grazed and year-to-year variations in precipitation patterns and snow cover.

The study area is on the northern edge of the grassland ecoclimatic province in Canada. It is a transitional zone between the more arid prairie to the south and the moister boreal forest to the north (Ecoregions Working Group 1989). Undisturbed areas are characterized by a mosaic of *Populus tremuloides* groves and *Festuca hallii* grasslands. Groves of trees occur on the wetter sites with shrub and grassland communities on the drier sites. Shrub communities are dominated by *Amelanchier alnifolia*, *Elaeagnus commutata*, *Rosa acicularis*, *Rosa woodsii* and *Symphoricarpos occidentalis*. *Festuca hallii* dominates open undisturbed sites but *Stipa curtiseta* co-dominates on grazed sites (Wheeler 1976). Recent research indicates that *Festuca hallii* is also the dominant in autumn grazed areas (Bailey et al. 1988). Other grasses characteristic of the area depending on site, aspect, moisture and disturbance include: *Agropyron smithii*, *Agropyron trachycaulum*, *Agrostris scabra*, *Bouteloua gracilis*, *Festuca saximontana*, *Koeleria macrantha*, *Helictotrichon hookeri* and *Poa pratensis*. *Artemisia frigida* was a characteristic woody increaser on disturbed sites.

This study was based on a long term grazing experiment developed and reported by Bailey et al. (1980b, 1988), and consisting of five long-term grazing regimes (Table 6.1). The purpose of this long-term grazing study was to compare the effects of grazing season (June vs Autumn) and grazing intensity (Light vs Heavy) with the widely practiced standard of Heavy Continuous grazing on a *Festuca-Stipa* grassland.

Each grazing regime was fenced to include 5.5 ha of grassland and a variable area of aspen forest and shrubland. Four randomly located 10 X 20 m exclosures were erected prior to commencement of grazing within the grassland portion of each regime. Two exclosures in each grazing regime were randomly selected for the etiolated regrowth study. Six cores of *Festuca hallii* were taken from inside (nongrazed samples) and six corresponding cores from outside (grazed samples) at the selected exclosures. The distance between each matching pair of cores was approximately 150 cm, or 75 cm in, or out, from the exclosure fenceline. The average core was 10 cm in diameter and 7 cm in depth. Using a custom manufactured soil coring device, the cores were collected at the end of the growing season on October 25, 1984 and October 12, 1985.

In October, visual note was made of uniformity of grazing and degree of grazing utilization for the Heavy and Light Autumn grazing regimes when the cores were collected.

Table 6.1. Long-term grazing regimes imposed on a *Festuca-Stipa* grassland in central Alberta (adapted from Bailey et al. 1988).

Grazing Regime (Year started)	Average Percent Use (%)	AUM's[1] Grazed	Period Grazed
Light June (1973)	32	8	June 1-30
Heavy June (1973)	61	24	June 1-30
Heavy Continuous (1976)	75	24	June 1- Sept 15
Heavy Autumn (1973)	67	24	Sept. 15 - Oct. 15
Light Autumn (1973)	37	8	Sept. 15 - Oct. 15

[1] AUM = Animal unit month

Etiolated Regrowth

In the greenhouse, each core sample was potted in a 15-cm pot, using potting soil, within 24 hours of field extraction. To stabilize the plants from any transplant shock prior to the start of the etiolated regrowth experiment, they were placed in the greenhouse for three weeks under controlled environment conditions. In 1984, the greenhouse conditions were 12 hours of light, a variable daytime temperature of 15 to 25° C and a minimum nightly temperature of 12° C, with weekly watering. In 1985, the same three-week daylength regime was intended, but a switch setting mistake caused the plants to receive three weeks of 24-hour light. The 1985 greenhouse temperature and watering regimes were the same as in 1984. After three weeks in the greenhouse the plants were all cut to a 2-cm stubble height to simulate the effect of grazing and then placed in a growth chamber with no light at 10° C. The 10° C temperature was selected to reflect growth conditions characteristic of a cool-season grass and to avoid the possibility that higher temperatures might inhibit regrowth for this species. The paired samples from each treatment were randomized within the growth chamber in order to minimize the effect of any environmental differences within the growth chamber. The samples were watered weekly, except when control of a mold problem required biweekly watering. Every third week, the etiolated regrowth was clipped at a 2-cm height, for a total of seven clippings (21 weeks) of etiolated regrowth. On November 25, 1984 a mechanical malfunction resulted in the growth chamber heating up to 40° C for 24 hours. This period of high temperature did not appear to affect the etiolated regrowth of the plants adversely. In 1984, the clipped material was separated into *Festuca hallii* and other species. In 1985, the clipped etiolated regrowth was separated into *Festuca hallii*, other grasses and grass-likes, as well as forbs and woody species.

Statistical Analysis

The mean dry weights of etiolated regrowth for the *Festuca hallii* and other material, for the cores from the inside and the outside of the two exclosures for each grazing regime, were summed for the 21-week regrowth period and expressed in mg pot^{-1} of etiolated dry matter. As the grazing regimes were nonreplicated in this experiment, a two-factor Model III analysis of variance was employed utilizing the simple treatment means for each year (Zar 1974). For this analysis, years are treated as random factor A and treatments are treated as a fixed factor B (Steel and Torrie 1980). This allows the testing of both the year and treatment factors by their interaction, assuming that there is no significant year-by-treatment interaction. In the event that there was a significant ($P<0.05$) year-by-treatment interaction, the test for treatments remains robust, but the test for years needs to be taken with caution (Zar 1974). Treatment means were separated using Duncan's new multiple range test to determine significant ($P<0.05$) differences (Steel and Torrie 1980).

RESULTS

Etiolated Regrowth

A year effect ($P<0.05$) for *Festuca hallii* and for the other species ($P<0.01$) was suggested (Table 6.2). However, the differences in the annual means for each treatment (Tables 6.3, 6.4) suggest a year-by-treatment interaction. The presence of this interaction is therefore assumed, and thus, the year factor cannot be adequately tested or discussed given the experimental design (Zar 1974).

There was a grazed versus nongrazed treatment effect ($P<0.01$) on the etiolated regrowth dry matter (DM) yield for *Festuca hallii* but not for other species ($P>0.05$) for the five grazing regimes (Table 6.2). The *Festuca hallii* etiolated regrowth means for the nongrazed and grazed treatments for the grazing regimes were separated with Duncan's new multiple range test (Tables 6.3).

For the nongrazed *Festuca hallii* treatments, the etiolated regrowth values for the Heavy June and Heavy Continuous grazing regimes were lower ($P<0.05$) than those from the Light Autumn grazing regime (Table 6.3). For the grazed *Festuca hallii* treatments, the etiolated regrowth from the Heavy June and Heavy Continuous grazing regimes were also lower ($P<0.05$) than for the Light Autumn grazing regime. The *Festuca hallii* etiolated regrowth for the grazed treatment was significantly lower ($P<0.05$) than the

Table 6.2 Mean square values of etiolated regrowth dry matter yield for nongrazed and grazed *Festuca hallii*, and nongrazed and grazed other species, in the Light June, Heavy June, Heavy Continuous, Heavy Autumn, and Light Autumn grazing regimes for 1984 and 1985.

Source	df	*Festuca hallii*	Other species
Year (Y)	1	685 *	2599 **
Treatment (T)	9	788 **	317
Error (Y x T)	9	126	174

* and ** indicate significant variances for $P<0.05$ and 0.01.

Table 6.3 Etiolated regrowth of *Festuca hallii* in the nongrazed (NG) and grazed (G) treatments of the Light June, Heavy June, Heavy Continuous, Heavy Autumn, and Light Autumn grazing regimes, with the percentage change of the etiolated regrowth in the grazed over nongrazed treatments of each grazing regime for 1984, 1985, and 1984 and 1985 combined.

	1984			1985			1984 & 1985 Combined		
Grazing Regime	NG mg pot^{-1}	G mg pot^{-1}	(G-NG)/NG %	NG mg pot^{-1}	G mg pot^{-1}	(G-NG)/NG %	NG mg pot^{-1}	G mg pot^{-1}	(G-NG)/NG %
Light June	52	24	-54	67	23	-66	60^{ab}	24^{cd}	-61
Heavy June	16	8	-50	60	11	-82	38^{bc}	10^{d}	-75
Heavy Continuous	36	11	-69	39	6	-85	38^{bc}	9^{d}	-77
Heavy Autumn	31	27	-13	60	23	-62	46^{abc}	25^{cd}	-46
Light Autumn	63	28	-56	77	46	-40	70^{a}	37^{bc}	-47

The same letter following means indicates no signifciant difference (Duncan's; $P \leq 0.05$).

Table 6.4 Etiolated regrowth of the other species in the nongrazed (NG) and grazed (G) treatments of the Light June, Heavy June, Heavy Continuous, Heavy Autumn, and Light Autumn grazing regimes, with the percentage change of the etiolated regrowth in the grazed over nongrazed treatments of each grazing regime for 1984, 1985, and 1984 and 1985 combined.

	1984			1985			1984 & 1985 Combined		
Grazing Regime	NG mg pot^{-1}	G mg pot^{-1}	(G-NG)/NG %	NG mg pot^{-1}	G mg pot^{-1}	(G-NG)/NG %	NG mg pot^{-1}	G mg pot^{-1}	(G-NG)/NG %
Light June	13	41	215	28	70	150	21	56	171
Heavy June	6	20	233	36	61	69	21	41	95
Heavy continuous	16	20	25	40	80	100	28	50	79
Heavy Autumn	31	43	39	33	43	30	32	43	34
Light Autumn	49	33	-32	54	55	2	52	44	-15

the nongrazed treatment for each grazing regime, with the exception of the Heavy Autumn grazing regime.

The percentage change ({[G-NG]/NG}*100) for etiolated regrowth of *Festuca hallii* of the nongrazed to grazed plants was always negative (Table 6.3). In sharp contrast, the etiolated regrowth of other species that were grazed was a positive increase of 171% over the nongrazed other species for the Light June regime (Table 6.4). For the Heavy June, Heavy Continuous and Heavy Autumn grazing regimes there were increases of 95%, 79%, and 34%, respectively, for the etiolated regrowth of the grazed plants versus nongrazed plants of other species. For the Light Autumn grazing regime, there was a small decrease (-15%) for etiolated regrowth of other species when grazed versus nongrazed treatments were compared. The percentage change for the nongrazed to grazed etiolated regrowth of other species progressively declined from the 170% increase for the Light June regime to the 15% decrease for the Light Autumn grazing regime (Figure 6.1).

In 1985, the etiolated regrowth was separated into *Festuca hallii*, other grasses and grass-likes, and forbs and woody species (Figure 6.2). For the grazed treatments the least etiolated regrowth for *Festuca hallii* occurred with the Heavy June and Heavy Continuous regimes and the greatest with the Light Autumn regime. For the other grasses and grass-like plants, the greatest etiolated regrowth was for plants in the Light intensity regimes and the

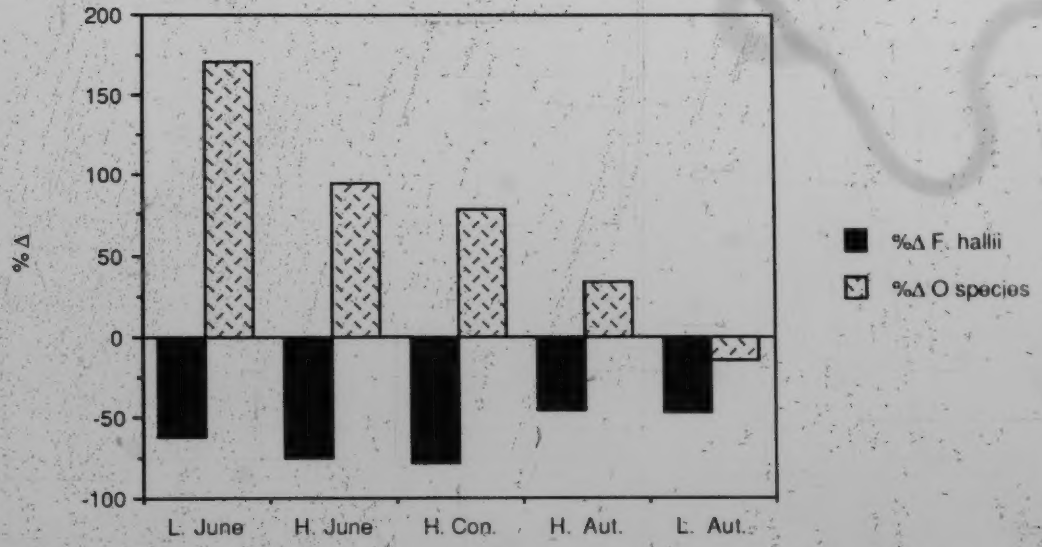

Figure 6.1 Percentage change (% Δ) for *Festuca hallii* and the other species for nongrazed to grazed etiolated regrowth for the Light June (L. June), Heavy June (H. June), Heavy Continuous (H. Con.), Heavy Autumn (H. Aut.) and Light Autumn (L. Aut.) grazing regimes. Data were combined for 1984 and 1985.

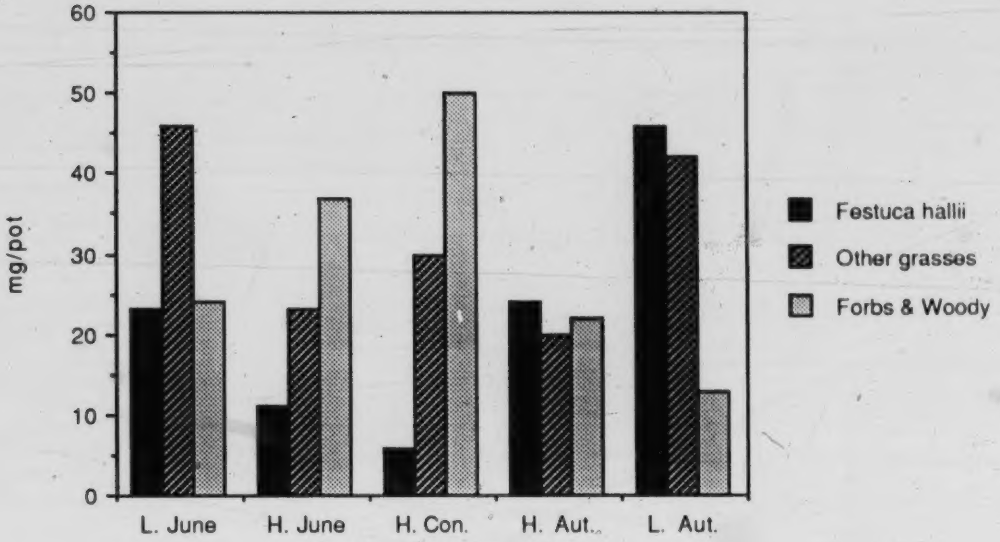

Figure 6.2 Etiolated regrowth of *Festuca hallii*, other grasses and grass-likes, and forbs and woody species for the Light June (L. June), Heavy June (H. June), Heavy Continuous (H. Con.), Heavy Autumn (H. Aut.) and Light Autumn (L. Aut.) grazing regimes for 1985.

least regrowth for the Heavy intensity regimes. For the forbs and woody species, the greatest amount of etiolated regrowth was for plants in the Heavy Continuous with the least regrowth for plants in the Light Autumn grazing regime.

DISCUSSION

Etiolated Regrowth of Nongrazed Plants

This study is based on the assumption that the plants from the nongrazed exclosures within each grazing regime would act both as a control between each grazing regime and within each grazing regime for the nongrazed versus grazed treatments. There was no difference ($P>0.05$) between grazing regimes for the etiolated regrowth of the nongrazed other species (Tables 6.2, 6.4). However, the results for the etiolated regrowth of *Festuca hallii* among the grazing regimes were different ($P<0.05$) (Tables 6.2, 6.3).

The nongrazed etiolated regrowth responses of *Festuca hallii* in the Heavy June and Heavy Continuous grazing regimes were lower ($P<0.05$) than those for the Light Autumn Grazing regimes (Table 6.3). For each grazing regime, the pattern of the nongrazed etiolated regrowth of *Festuca hallii* followed that of the grazed treatments. These observations suggest that the etiolated regrowth response of *Festuca hallii* within the exclosures was affected by the surrounding grazing regime.

The mechanism for this exclosure effect may be associated with modification of the surrounding water dynamics by the long term heavy grazing regimes, thereby affecting the microenvironment surrounding the exclosures. Naeth (1988) found at Kinsella, that intensity of grazing had a greater detrimental effect on soil water and the water holding capacity of standing litter, than season of grazing. Given that the nongrazed samples were extracted approximately 0.75 m inside the exclosure fenceline, their available water may have been affected by the surrounding long term heavy intensity grazing regimes thereby reducing the vigor of these nongrazed plants compared with the nongrazed plants taken from the long term light intensity grazing regimes.

The differences discussed above indicate that for *Festuca hallii*, comparisons among grazing regimes must be conducted with care as the etiolated regrowth of the nongrazed plants from within the exclosures was likely affected by the surrounding grazing regimes.

For the etiolated regrowth of the nongrazed other species, there were no significant differences among grazing regimes (Tables 6.2, 6.4). Therefore, the nongrazed etiolated regrowth of the other species may be used with relative confidence as a control between the grazing regimes. There was a trend for the yield values for the etiolated regrowth of the nongrazed other species to increase from the Light June to the Light Autumn grazing regimes. This may indicate that the autumn grazing regimes enhanced the etiolated regrowth of the other species within the exclosures compared to that from the spring grazing regimes.

Etiolated Regrowth of Grazed Plants

For the grazed *Festuca hallii*, the etiolated regrowth results for the Heavy June and Heavy Continuous grazing regimes were lower (P<0.05) than those for the Light Autumn grazing regime (Table 6.2, 6.3). These results are similar to those for the nongrazed treatments as discussed above. The difference between Heavy June and Light Autumn regimes suggests that the effects may be associated with the interaction of intensity and season of grazing for *Festuca hallii*. There were no significant differences in the etiolated regrowth of *Festuca hallii* between the Light and Heavy intensity regimes for either the June or Autumn periods. In both cases, however, the High intensity regime resulted in a reduction of etiolated regrowth compared to the Light intensity regime suggesting a reduction in vigor with increasing grazing intensity. This reduction in etiolated regrowth only became significant, however, when the interaction of season was added, which suggests that autumn grazing resulted in less vigor loss than June grazing.

There were no significant differences in etiolated regrowth for the grazed other species among the grazing regimes suggesting that their combined vigor was not as sensitive to intensity or season of grazing as that of *Festuca hallii* (Tables 6.2, 6.4). This lack of significant difference, however, does not reflect the shifts in species composition for the other species associated with the long-term effects of intensity or season of grazing as noted by Bailey et. al. (1988).

Etiolated Regrowth of Grazed versus Nongrazed Plants

As discussed above, the interaction of season and intensity of grazing provides a logical explanation for the etiolated regrowth pattern between the grazing regimes for the grazed *Festuca hallii* plants. The percentage change in the etiolated regrowth for the grazed versus nongrazed *Festuca hallii* for each grazing regime, however, raises another possible hypothesis that intensity of grazing had a greater effect on *Festuca hallii* plants than season of grazing.

The evaluation of the nongrazed and grazed treatment differences within each grazing regime must be interpreted carefully as the etiolated regrowth responses from the nongrazed *Festuca hallii* plants in the Heavy intensity regimes may have been affected by the surrounding grazing regimes as discussed earlier. This could result in a low estimation of the potential differences between the nongrazed versus grazed treatments for the heavy intensity grazing regimes.

The greatest percentage decrease for the etiolated regrowth of *Festuca hallii* was for grazed plants in the Heavy June and Heavy Continuous regimes (Table 6.3). This was despite the fact, that etiolated regrowth from nongrazed plants in these regimes was the lowest, thereby minimizing the magnitude of the percentage change for these regimes (Table 6.3, Figure 6.1). If the exclosures had been larger than 10 X 20 m or the plant samples had been taken from the center of the exclosures instead of 0.75 m inside the exclosure's fenceline, it might have been possible to minimize or eliminate the effects of the surrounding grazing regime on the plants inside the exclosure. It might have been possible then to show that the effect the heavy intensity grazing regimes had on the percentage change in etiolated regrowth between the grazed and nongrazed *Festuca hallii* plants would have been larger. If the etiolated regrowth for the nongrazed *Festuca hallii* plants was averaged and considered to be equal for each regime, then the percentage reduction for the grazed plants in the Heavy Autumn regime would be similar to the percentage reduction for the Light June regime. This would then suggest that the Heavy June and Heavy Continuous grazing regimes caused the greatest reduction in vigor for *Festuca hallii* while the Light June and Heavy Autumn grazing regimes would result in intermediate but similar reductions in vigor. The Light Autumn grazing regime, however, would still result in the least vigor loss for *Festuca hallii*. This would suggest a grazing regime order for decreasing defoliation stress of: Heavy Continuous, Heavy June, Light June, Heavy Autumn, and Light Autumn. This order is consistent with species richness versus grazing stress observations for these same grazing regimes made by Bailey et al. (1988).

The percentage change in etiolated regrowth between the nongrazed and grazed plants of other species among the different grazing regimes shows what is perhaps the most important finding of this study (Table 6.4, Figure 6.1). The percentage change for the nongrazed to grazed etiolated regrowth of other species remained positive, but progressively declined, for the Heavy June, Heavy Continuous and Heavy Autumn grazing regimes, before dropping to a negative change of -15% for the Light Autumn grazing regime.

The dramatic increase in the vigor of the other species for the Light June grazing regime may reflect two factors. The first factor is likely the differences in timing of maximum growth rates between *Festuca hallii* vs the other species. For *Festuca hallii* the maximum rate of growth appears to be in May and June while the maximum rate of growth for the other species appears to be June and July (Chapter III, Willoughby et al. in prep.). The second factor is intensity of grazing. Under light June grazing a greater proportion of *Festuca hallii* will be selectively grazed than the other species. This combination of factors is probably an ideal situation for the competitors of *Festuca hallii*. *Festuca hallii* is selectively utilized during its maximum growth phase while leaving the other species only lightly used at the beginning of their maximum growth phase. The sensitivity of *Festuca hallii* to season of defoliation is also indicated by the reduction of tiller numbers in response to defoliation during the early June period versus early May or early July (Chapter IV).

The vigor of the other species was clearly favored by the June grazing regimes compared to the autumn grazing regimes (Figure 6.1). The decline in the etiolated regrowth of the other species for the Heavy June compared to the Light June grazing regimes was likely reflecting the change in grazing intensity. Under the Heavy Continuous and Heavy Autumn grazing regimes the other species were also being grazed intensively with an associated decrease in vigor in comparison to the Light June regime.

If the influence of the Heavy Autumn grazing regime on the etiolated regrowth of the nongrazed *Festuca hallii* plants from within the exclosures was removed, the results would likely have shown a greater decline in vigor for the grazed *Festuca hallii* plants from the Heavy Autumn compared to the Light Autumn grazing regimes (Table 6.3, Figure 6.1). This anticipated greater decline in vigor would be likely associated with the differences in grazing intensity between the two Autumn regimes. *Festuca hallii* would appear to be most vigorous under the Light Autumn grazing regime and therefore would be most competitive with the other species under this type of grazing regime.

The response of *Festuca hallii* to any grazed versus non-grazed treatment in all the regimes was a decline in vigor as measured by etiolated regrowth. This decline would be anticipated for a decreaser species in this grassland (Bailey et al. 1988, Wroe et al. 1988). In contrast, with the exception of the Light Autumn grazing regime, the general response of the other species to grazing versus nongrazing was an increase in vigor as measured by etiolated regrowth. This response of other increaser species could be expected, particulary for the Heavy intensity regimes. Looking at the percentage change in etiolated regrowth for both the *Festuca hallii* and other species together clearly shows the Heavy June and Heavy Continuous grazing regimes as the most damaging to the vigor of *Festuca hallii* (Figure 6.1). The Light June grazing regime while somewhat less detrimental to the vigor of *Festuca hallii* when compared to the Heavy June and Heavy Continuous grazing regimes, allowed the maximum increase in vigor of the other species. This may indicate that Light June grazing has the potential to cause as great a decline in range condition as Heavy June grazing by maximizing the vigor of other species.

The Heavy Autumn grazing regime showed a minimum reduction in vigor for *Festuca hallii* while simultaneously showing the least increase in the vigor for the other species (Figure 6.1). The Light Autumn grazing regime, however, would appear to be the best grazing regime in terms of minimizing the effect of defoliation on *Festuca hallii*, while simultaneously minimizing the increase of vigor for the other species. The Light Autumn grazing regime clearly gave *Festuca hallii*, as a decreaser, the greatest competitive advantage against the other species. Therefore this would be the grazing regime most likely to maintain the optimum range condition based on the results of this study. This study did not allow for the problems associated with selective grazing and uneven utilization which were visually observed in the Light Autumn grazing regime at a grazing intensity of 8 AUM's. This research does clearly indicate that Light Autumn use is the best grazing regime of the five grazing regimes studied. However, further research is required to determine the optimal autumn stocking rate between the selective grazing losses associated with 8 AUM's and the reduction of range condition associated with the increased vigor of other species associated with 24 AUM's.

Species Composition of Etiolated Regrowth in 1985

The clipped etiolated regrowth was separated into *Festuca hallii*, other grasses and grass-likes, and forbs and woody species in 1985 (Figure 6.2). These results indicated clearly that the etiolated regrowth for the other species under the two Light intensity grazing regimes was proportionately more grass species than forbs or woody species. In contrast, there was a greater proportion of etiolated regrowth of forbs and woody species versus other grasses and grass-likes for each of the Heavy intensity grazing regimes. This shift in the relative components of the other species for the Light versus Heavy intensity grazing regimes indicated that the Heavy intensity grazing regimes favored an increase in dicotyledon invader species. In contrast, the low intensity grazing regimes appeared to favor an increase of monocotyledon increaser species. The component proportions of the etiolated regrowth for the Light Autumn grazing regime again suggested that this was the best grazing regime for maintaining good range condition.

CONCLUSIONS

This study has demonstrated that the amount of etiolated regrowth from autumn collected samples reflected the expected effects of historic long term grazing regimes as described by Bailey et al. (1988). This suggests that given an adequate etiolated regrowth data base for a given species for a given geographic region, etiolated regrowth measurements could be used as a technique or diagnostic tool for determining the historic grazing practices on grasslands where records of those practices do not exist or are under dispute.

This study also demonstrated that great care must be used in selecting the size of exclosures and in the selection of sampling location within exclosures to minimize or eliminate the effects of the surrounding grazing regime on the ungrazed samples.

Festuca hallii is clearly a decreaser species and is most susceptible to loss of vigor when grazed during June and with Heavy Continuous grazing. *Festuca hallii* had the greatest vigor following autumn grazing regardless of the grazing intensity.

The Light Autumn grazing regime was the best of the five grazing regimes studied for maintaining the vigor of *Festuca hallii*. The results of this study indicate that a grazing regime order for decreasing defoliation stress on *Festuca hallii* would be: Heavy Continuous, Heavy June, Light June, Heavy Autumn, and Light Autumn.

Further research is required to determine the optimal autumn stocking rates between the production losses of *Festuca hallii* associated with selective grazing at 8 AUM's and the loss of range condition caused by the increased vigor of other species associated with autumn grazing at 24 AUM's.

Other species appear to be given the greatest competitive advantage over *Festuca hallii* under Light June grazing and the least competitive advantage under Light Autumn grazing. High intensity grazing regimes favored the vigor of forbs over grasses whereas the low intensity grazing regimes favor the vigor of grasses over forbs, especially during the autumn grazing season.

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VII. RESEARCH SYNTHESIS

This research project has demonstrated some effects of season, frequency, and intensity of defoliation on *Festuca hallii* in central Alberta. *Festuca hallii* is the dominant perennial native grass in the *Festuca-Stipa* grasslands of the Aspen Parkland ecoregion of Western Canada (Strong and Leggat 1981, Pavlick and Looman 1984). As a native species, it has adapted over time to the climatic, edaphic and herbivorous features of the western Canadian prairies. It would be reasonable to deduce, therefore, that some of the growth cycle features and defoliation treatment responses found in this research reflect certain historical adaptation characteristics of *Festuca hallii*. As part of the Festuceae tribe, *Festuca hallii* is historically part of the Arcto-Tertiary Forest complex of vegetation which developed in the temperate part of North America during the Paleocene epoch (Dix 1964).

GROWTH AND FORAGE QUALITY FACTORS OF *Festuca hallii*

Festuca hallii is characterized by both rapid growth and rapid phenological change from the middle of April to the end of June (Chapter III). In terms of long term climatic patterns in central Alberta, optimum moisture conditions occur from April to June, with June being the only month when long-term precipitation exceeds potential evapotranspiration (Chapter II). For the July, August and September period there is a substantial potential evapotranspiration deficit compared with the April, May and June period. Therefore the speed of biological change in *Festuca hallii* between mid April and June suggests that it is adapted to take optimum advantage of the normally prime moisture conditions from April to June. Its vulnerability to intense June defoliation (Chapter IV, VI), or frequent spring defoliation (Chapter V) suggests that this plant was not historically exposed to intense late spring defoliation. This suggestion would be consistent with the nineteenth century observations that the plains buffalo made a southerly migration out of the parkland to the open plains to the south with the approach of summer, while in the winter they would return north to obtain the shelter of the hummocks and woodlands of the parkland region (Roe 1970). When a single intense defoliation was applied at the beginning of June it resulted in a reduction of tiller density compared to the same treatment at the beginning of July (Chapter V). When both heavy and light grazing were applied for the entire month of June, there was not only a reduction of the vigor of *Festuca hallii*, but a progressive increase of the vigor of the other species in the sward with increasing intensity of grazing (Bailey et al. 1980, Bailey et al. 1988). These observations together suggest that both *Festuca hallii*, and the *Festuca-Stipa* grassland community of the Aspen Parkland, were not adapted historically to intense extended grazing in the late spring.

Festuca hallii appears to have two particular forage quality characteristics that make it both comparable to, and distinguished from, some of the higher yielding exotic species that have been introduced to the western Canadian prairies. From May to July crude protein (%) was at levels equal to that of certain exotic grasses, and from July onwards was superior to the levels found in those introduced exotics (Chapter III). The crude protein (%) curve plateaued at about 8.5% from the beginning of July until some point in September, 1987. Since 1987 was a comparatively dry year, late summer and early autumn yields were lower than those of 1986, 1988 and 1989 (Chapters IV, V, Willoughby et al. in prep.). This suggests that during a wetter year the crude protein (%) plateau may extend further into the autumn than it did in 1987. The 1987 results from this study indicate no loss of crude protein yield untill late summer (early September). This contrasts with the response of certain exotics, such as *Phleum pratense*, where crude protein (%) and crude protein yield decline late in the growing season, unless the plants are defoliated in the late spring (Johnston and Bezeau 1962).

The second forage quality characteristic which appears to distinguish *Festuca hallii* from all other northern great plains forage grasses reported in the literature to date, is that the percentage of acid detergent lignin is very low throughout the growing season. It was only 3% at the end of the 1987 growing season (Chapter III). In addition, work with nuclear magnetic resonance suggests that the degree of ether cross-linking in the lignin-cellulose complex for *Festuca hallii* is lower than in other forage grasses. Both these lignin features would suggest that the dormant season digestibility of *Festuca hallii* should be greater than other species which have higher acid detergent lignin (%) and higher degrees of ether cross linkages in their lignin-cellulose complexes. These features of *Festuca hallii* lignin would therefore suggest a species adapted for late summer, autumn, and winter (weathered) grazing. This would fit with the historic pattern of the plains buffalo moving into the Aspen Parkland ecoregion with the approach of winter.

SWARD RESPONSES

Sward composition (DM%) remained in a steady state for the growth cycle independent of the variable growth rates of the different sward components (Chapter III). In the season of defoliation experiment, only the sward composition of *Festuca hallii* in the May treatment was higher than that in the other treatments for both years (Chapter IV). This probably reflects the comparatively early spring growth cycle for *Festuca hallii* compared with other species (Chapter III). None of the season of defoliation treatments were significantly different from the control or burnt control in either year, again indicating a relatively steady state for sward composition within the time frame of this study. This suggests that under the comparatively dry growing conditions of this three year study, a single annual defoliation treatment does not have a major effect on sward composition. This preliminary result, however, needs to be tested over a longer time frame (e.g. ten years) which would include years with normal or above normal precipitation.

The frequency of defoliation experiment demonstrated a clear and progressive decline in sward composition for *Festuca hallii* with increasing frequency of defoliation (Chapter V). This decline was associated with a dry matter yield (DMY) reduction for *Festuca hallii*, whereas the DMY of the other grasses and grass-likes, forbs, and woody species components were not significantly affected by increasing frequency of defoliation. The frequency of defoliation effects were in sharp contrast to the much smaller changes in sward composition of *Festuca hallii* in the season of defoliation experiment (Chapters IV). These results suggest that frequency of defoliation is of greater importance than season of defoliation when the defoliations are applied at the same intensity and duration. For the grazing season by intensity experiment, the month-long autumn grazing period was clearly preferable to the month-long June grazing period for maximizing the sward composition of the etiolated regrowth of *Festuca hallii* (Chapter VI). The light intensity grazing treatments also had a higher sward composition of *Festuca hallii* etiolated regrowth than that of the heavy intensity grazing treatments. In summary, frequency of defoliation would appear to be more important than season of defoliation for reducing sward composition of *Festuca hallii* where mowing treatments have been applied for 3 consecutive years.

Season would appear to be more important than intensity for reducing sward composition in the long-term grazing experiment where month-long grazing treatments were applied for 12 consecutive years.

The period of maximum crop growth rate for *Festuca hallii* appears to be in May (Willoughby et al. in prep.) which would coincide with the period of long term optimum moisture conditions as discussed earlier (Chapter II). Annual *Festuca hallii* DMY is also sensitive to year-to-year differences in growing season precipitation patterns (Chapter IV, V).

For the season of defoliation experiment, DMY appeared to be influenced more by the timing of growing season precipitation than the season of defoliation treatments (Chapter IV). The significant season of defoliation yield differences in 1986 were associated more with substantial differences in month to month precipitation amounts than with a season of defoliation treatment effect. There were no season of defoliation effects in 1987 . This suggests a season of defoliation resilience on the part of *Festuca hallii* for DMY when subjected to a single annual intense mowing defoliation.

The frequency of defoliation experiment clearly indicated that more than two cuts per growing season will result in a reduction of DMY. Year-to-year differences in precipitation may also generate differences in the regrowth patterns following defoliation. June precipitation appears to be very critical for subsequent regrowth in a multiple cut system. Duration of vigor rest for optimum DMY would appear to be at least 8 weeks for intense defoliations. This suggests that *Festuca hallii* is adapted to a high intensity low frequency type of defoliation system.

For the grazing season by intensity experiment, the month-long autumn grazing treatments were preferable to the month-long June grazing treatments in terms of maximizing the vigor or etiolated regrowth of *Festuca hallii* (Chapter V). *Festuca hallii* vigor was also higher in the light intensity grazing treatments. The season factor appears to have had a greater impact than the intensity factor on the vigor or etiolated regrowth of *Festuca hallii*. This again suggests that for defoliation events of the same duration (e.g. a one month grazing period), season is more important than intensity in terms of effect of defoliation on *Festuca hallii*.

***Festuca hallii* RESPONSES**

Inflorescence density of *Festuca hallii* was variable from year to year as demonstrated in the variable responses of the control from 1986 to 1987 for both the season of defoliation and the frequency of defoliation experiment (Chapter IV, V). There was also a trend for the inflorescence density in the burnt control to be higher than that of the control in both defoliation experiments. This would imply that the litter removed by the prescribed burn of May 1985 directly, or indirectly, enhanced inflorescence production when compared to that of the control.

There were no differences in inflorescence density of *Festuca hallii* among the season of defoliation treatments in 1986. In 1987, the inflorescence density in the burnt control and October season of defoliation treatments were higher than for those in the July and August treatments. There was a trend over both years for the July defoliation treatment to suppress inflorescence production. Conversely there was a trend for the inflorescence density in the September and October defoliation treatments to be higher than that in the July defoliation treatment. The inflorescence density in the August defoliation treatment exhibited a variable response. This indicates that defoliation in early July suppresses floral initiation. Defoliation in early August may or may not influence floral initiation for the following year. These results are consistent with the August to early September period for floral initiation which was determined for *Festuca campestris* (Johnston and McDonald 1967). Therefore if a high inflorescence density is desired for improvement of range condition or seed production, defoliation from May to early September should be avoided.

Tiller density was significantly affected by both the season of defoliation and frequency of defoliation experiments. Only two treatments in the season of defoliation experiment and one treatment in the frequency of defoliation experiment were significantly different from the burnt control. This suggests that tiller density may be fairly robust to changes in defoliation stress and therefore an important indicator of significant shifts in degree of defoliation stress.

Tiller density of *Festuca hallii* in the June defoliation treatment was significantly lower than the tiller density of plants in the burnt control in the season of defoliation experiment (Chapter IV). The reduction in tiller density for plants in the June treatment would suggest a level of defoliation stress that could be expected given the rapid rate of growth and phenological change which occurred in the plants during the May to June period (Chapter III). This reduction in tiller density of *Festuca hallii* is an important clue to defoliation stress during this period of the growing season as there was no significant corresponding reduction in DMY for the June treatment when compared to that of the other season of defoliation treatments. In contrast, the October defoliation treatment had a significantly higher tiller density than the burnt control. This defoliation occurred at the end of the growing season and would therefore, presumably, impose the least stress on the plants (Chapters III, IV, VI). The plants in the July defoliation treatment had significantly higher tiller densities than the plants in the June defoliation, which had the lowest tiller density. This major change in tiller density within a four week period from early June to early July indicates a fundamental shift in degree of season of defoliation stress. This suggests that *Festuca hallii* is more vulnerable to defoliation at the beginning of June compared to the beginning of July. Therefore timing of initial growing season defoliation should be delayed till the beginning of

July in order to minimize spring defoliation stress. Defoliation between early May to late June should be avoided completely.

For the frequency of defoliation experiment, only the 8-cut defoliation treatment had a significantly lower tiller density than the burnt control, despite reductions in sward composition and DMY for *Festuca hallii* in the 4-cut defoliation treatment (Chapter V). This suggests that tiller density is a more robust indicator of defoliation stress than total DMY and sward composition which are also influenced by precipitation amount and distribution.

For the season of defoliation experiment, the end-of-season stem base DM weight, total nonstructural carbohydrate (TNC) percentage, TNC pool, and root DM weight to the 7.5 cm depth, were not affected by the season of defoliation treatments. This was in sharp contrast to the frequency of defoliation experiment where end-of-season stem base DM weight, TNC pool, and root DM weight all decreased significantly with increasing frequency of defoliation. This indicates that *Festuca hallii* has a degree of resilience to single annual high intensity defoliations which is independent of the time of defoliation within the growing season for these parameters.

DEFOLIATION TREATMENT EFFECTS

Overall, in contrast to the effects generated by the frequency of defoliation experiment, few significant results were generated from the effects of season of defoliation on *Festuca hallii* after two or three years of treatment with single annual intense defoliations at the beginning of each month of the growing season. This raises the question, as noted in different sections above, of whether frequency of defoliation may therefore be of greater management importance for *Festuca hallii* than season of defoliation when using the intense short duration defoliation events imposed by a mower. The long term grazing season and grazing intensity experiment clearly suggests that grazing season is of greater importance than grazing intensity when using month-long grazing periods. While the defoliation techniques are fundamentally different between the mowing and grazing studies, the results do suggest the possibility of ordering the defoliation factors by their descending impact on the biology of *Festuca hallii*. A proposed hypothesis would be: frequency of defoliation > season of defoliation > intensity of defoliation. The testing of this hypothesis would require a defoliation technique of standardized duration which was not accomplished in this research programme with the mixing of mowing and grazing studies. It would also require the use of a defoliation experiment which was repeatable through a sequence of different phases within the growing season. This would enable the comparison, for example, of a 4-cut frequency of defoliation system with a 4-week duration of rest that was started at the beginning of May versus the beginning of June, versus the beginning of July. This type of experiment would then allow the comparison of frequency of defoliation effects within the context of a season of defoliation framework.

MANAGEMENT IMPLICATIONS

This research has confirmed that *Festuca hallii* is the key species for the effective management of the *Festuca-Stipa* grassland of the Fescue prairie association of central Alberta. Determining the best defoliation management for this species is of economic importance because this region supports at least 30% of the Alberta beef herd. The optimum management of this species is also of critical importance in terms of the effects of season, frequency and intensity of defoliation if the ecological health, or range condition, of *Festuca-Stipa* grasslands are to be maintained or improved. Some of the management suggestions that can be drawn from the scientific insights synthesized from this research are as follows.

1. Utilization of *Festuca hallii* for early spring grazing during April would appear to be safe, provided the plants are not subsequently grazed through the critical May and June growing period of the same year.

2. Late spring (early May to late June) grazing should be avoided with defoliation preferably delayed till after July 1st. Defoliation during the critical spring growth period from early May to late June should be avoided given the rapid

growth of *Festuca hallii* at this time, its loss of tiller and inflorescence density with defoliation during this period, and the competitive advantage given to other sward components with defoliation during June.

3. Late summer and autumn grazing may be used to some advantage because of the nutritional quality characteristics of *Festuca hallii.* Protein DMY for this plant peaks late in the growing season and is combined with a low lignin content throughout the growing season. These are important features when planning management objectives for complementary grazing systems which include *Festuca-Stipa* grasslands.

4 Swards dominated by *Festuca hallii* may be suited to a high intensity-low frequency or short duration types of grazing systems with an initial grazing during July, followed by another grazing in October, and then through the winter as snow cover permits. This suggestion is based on the following observations. The plant appears to be relatively resilient to short duration high intensity defoliations. A defoliation frequency of no more than 2-cuts per growing season with a minimum vigor rest of eight weeks is optimal for DMY. The July and October periods are the two periods of the growing season during which *Festuca hallii* appears to be most resistant to defoliation stress.

5. Inflorescence induction and density on sites that have been undisturbed for long periods of time with a long standing

litter buildup are enhanced by the removal of that litter with a prescribed burn.

6. Inflorescence induction and density are also enhanced by deferring defoliation to a single annual intense defoliation event which occurs after the beginning of September and preferably after the beginning of October.

7. Tiller density of *Festuca hallii* was enhanced by a single annual intense defoliation limited to early July or after the beginning of October.

8 Tiller density of *Festuca hallii* was increased by a prescribed burn in May on a *Festuca-Stipa* grassland which had a high degree of litter buildup associated with years of no-grazing.

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